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BRITISH MUSEUM (NATURAL HISTORY)

INSECTS OF SAMOA

AND OTHER SAMOAN TERRESTRIAL ARTHROPODA

PART IX. SUMMARY

FASC. 2. Pp. 33–104

By Professor P. A. BUXTON

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INSECTS OF SAMOA

AND OTHER SAMOAN TERRESTRIAL ARTHROPODA

Although a monograph, or series of papers, dealing comprehensively with the land arthropod fauna of any group of islands in the South Pacific may be expected to yield valuable results, in connection with distribution, modification due to isolation, and other problems, no such work is at present in existence. In order in some measure to remedy this deficiency, and in view of benefits directly accruing to the National Collections, the Trustees of the British Museum have undertaken the publication of an account of the Insects and other Terrestrial Arthropoda collected in the Samoan Islands, in 1924–1925, by Professor P. A. Buxton and Mr. G. H. E. Hopkins, during the Expedition of the London School of Hygiene and Tropical Medicine to the South Pacific. Advantage has been taken of the opportunity thus afforded, to make the studies as complete as possible by including in them all Samoan material of the groups concerned in both the British Museum (Natural History) and (by courtesy of the authorities of that institution) the Bishop Museum, Honolulu.

It is not intended that contributors to the text shall be confined to the Museum Staff or to any one nation, but, so far as possible, the assistance of the leading authorities on all groups to be dealt with has been obtained.

The work is divided into nine "Parts" (see p. 3 of wrapper), of which each is subdivided into "Fascicles." Each of the latter, which appear as ready in any order, consists of one or more contributions. On the completion of the systematic portion of the work it is intended to issue a general survey (Part IX), summarising the whole and drawing from it such conclusions as may be warranted.

A list of Fascicles already issued will be found on pp. 3 and 4 of this wrapper.

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INSECTS OF SAMOA

Part IX, Fasc. 2

SUMMARY

By P. A. Buxton

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I. THE INSECT FAUNA: ITS COMPOSITION

Introductory

We have already (ix, 19) discussed zoogeography, excluding the insects. The evidence shows clearly that the fauna and flora reached Samoa from the west. It appears that there is little evidence of the former existence of a large land mass in the area now occupied by tropical Polynesia.

It now remains to discuss the evidence that may be derived from a study of the Samoan insects, and it may be said that the other terrestrial Arthropoda appear to give little help in this connection. Even with the insects what can be done is limited, for we have so little knowledge of other archipelagos with which to compare the Samoan fauna. Two considerable groups of islands, both of them containing "high" volcanic islands with a rich flora and fauna, lie relatively near to Samoa. To the west is Fiji: to the south and south west, Tonga. The insect fauna of Fiji is fairly well investigated but only so far as some groups are concerned. There is, for instance, the book by Bezzi (1928) on the Diptera, excluding the Nematocera, and there are a number of papers by Kirkaldy and others on the Heteroptera; but no comprehensive study of the Fijian insects has ever been attempted. As to Tonga, much less collecting has been done, and our knowledge is extremely imperfect and fragmentary; indeed, I do not know any important group of Tongan insects which has been thoroughly investigated. What is known about other archipelagos which lie farther from Samoa is of less assistance to us. The Pacific Entomological Survey has made large collections in the Marquesas, and the results are now coming from the press as Bulletins of the Bishop Museum in Honolulu. A preliminary general description of the Marquesas has been published by Mumford and Adamson (1934), from which it appears probable that the relation between Marquesan and Samoan insects is not close. It is, of course, well known that the insects of the Hawaiian group have been very fully investigated. Apart from the classical Fauna Hawaiiensis, there are a large number of papers in the *Proceedings of the Hawaiian Entomological Society;* Bryan (1934) has recently published a census of the fauna, showing the number of endemic and other species, order by order. But Hawaiia is so remote from the rest of Polynesia, and its fauna is so peculiar that direct comparisons between it and Samoan insects cannot be made.

As there is so little with which our fauna can be compared, the present

summary is not final but provocative: it is my intention to suggest subjects which demand study in the field, which is preferable to the collection of more insects.

The Material

The *Insects of Samoa* is based upon all material which was available. The nucleus was a collection formed by G. H. E. Hopkins and myself during our stay in Samoa, which lasted throughout 1924 and 1925. We were working there for the London School of Tropical Medicine, as it was then called, and we were only able to work in the field as opportunity arose. But we collected steadily on the island of Upolu, from the coast at Apia to the rain forest at about 2,000 feet round the rest-house at Malololelei. Our collections in this part of Upolu were made at all seasons of the year, but the work was done on occasional days and half days, when we could spare the time. We also made small collections on Savaii and Tutuila, and on several of the small islands which lie off the east coast of Upolu. Our collection was thought to amount to about 20,000 specimens. Where specimens are enumerated in the systematic parts of this work, and no collector's name is given, it is to be assumed that they were collected by Mr. Hopkins and myself. Our friend, Dr. J. S. Armstrong, made a collection principally on Upolu between the years 1921 and 1926. All types and unique specimens in his collection and ours have been placed in the British Museum (Natural History).

The material which I have mentioned has been supplemented by all the Samoan material in the Bernice P. Bishop Museum, Honolulu, which was put at our disposal by the authorities of that institution: about 6,000 specimens were received from Honolulu. This material included collections made by O. Swezey and G. F. Wilder, who collected at Pago Pago, Tutuila and, to a less extent, in other parts of Samoa in 1923. With their material were the insects collected by E. H. Bryan in 1924. Mr. Bryan worked on all the three main islands, and his collection is especially valuable because he reached a height of about 5,000 feet on Savaii: no other Samoan material from any altitude beyond 2,000 feet has been available. Mr. A. F. Judd has also collected in Samoa, particularly in the Manua Group, and his specimens were also forwarded from Honolulu: no other considerable collections have been made in the Manua Islands. A collection made by Dr. H. C. Kellers on Tutuila and other parts of the group in 1918 was sent to us by the Experiment Station of the Hawaiian Sugar Planters

Association by the kindness of the late Mr. Muir ; I understand that this material has now been incorporated in the Bishop Museum's collection. Several of the collectors from Honolulu were expert in obtaining the obscure insects found in the wet mountain forests of those islands ; this fact made their Samoan collections particularly valuable. On the other hand it should be recorded that no one collector spent much time on several islands, which is regretted because the skill and experience of the individual count for so much. The collections from different islands in Samoa are not therefore quite comparable.

Types and unique specimens received from Honolulu have been returned to the Bishop Museum. There has been a free interchange between that institution and the British Museum of duplicate material, and both institutions have benefited greatly from this arrangement.

The British Museum (Natural History) contains a number of small collections made in Samoa, some of them many years ago. Among them one may mention Lepidoptera sent home by the Rev. C. Whitmee, P. de la Garde, J. Lister, and G. F. Mathew ; Dr. H. Swale's beetles ; and a number of insects of several orders collected by Dr. F. W. O'Connor. The authors of certain portions of this work have made use of other Samoan material. Specimens from Hamburg, Vienna, Tring, Oxford, and several American collections have been examined and utilized.

It will be observed that, owing to friendly collaboration with the Bishop Museum, a large amount of material has been available from all the principal islands of the Samoan Group, with the exception of Rose Atoll. This exception is of no material importance, for the atoll is utterly unlike the high, fertile, volcanic islands which compose the rest of Samoa, and only four sorts of flowering plants grow upon it (Mayor, 1924). We may, therefore, assume that its land fauna is negligible : except in name it is no part of Samoa.

The collections were made on all the Samoan islands, and at all seasons ; it may well be asked whether they afford a fair sample of all orders of insects. In this matter I can speak definitely for Mr. Hopkins and myself, and we accumulated the greater part of the material. It was our fixed intention to collect insects of all orders, trusting that some channel of publication would be discovered if an adequate general collection were brought home. But in point of fact, two men, working only in their spare time, cannot devote attention to all insects, even in an oceanic island ; one tends to see and collect those groups of insects with which one is specially acquainted, or those about which some

correspondent at home is frequently writing. I should say that Hopkins and myself were least successful in obtaining Coleoptera, Thysanoptera and parasitic Hymenoptera; we obtained fair but not good collections of most families of Hemiptera, Hymenoptera (excluding Parasitics), Diptera (excluding Nematocera), and most of the small orders of insects and of the terrestrial Arthropods. In the following groups we obtained our best collections :—Orthoptera (especially Gryllidae), Fulgoroidea, Lepidoptera (including Microlepidoptera *), Nematocera, Isoptera and Neuroptera; the Odonata were carefully collected by Armstrong. Among the other classes of terrestrial Arthropoda, we made a large collection of Araneida. The collections of Myriapoda and terrestrial Isopoda were not good; no collection of Acarina was made.

The fact that a considerable number of specimens were collected by other entomologists has been of the greatest service, and I believe that the material as a whole is a very fair sample of the insect fauna of the Samoan Islands. If further exploration becomes possible, I think that particular attention should be devoted to the Coleoptera †, the Diptera Athericera, and the insects inhabiting soil (at present unknown ‡).

We have been so fortunate as to find experts who were willing to deal with all the material which was collected, except only the parasitic Hymenoptera. Even in that group it would have been possible to identify certain parts, but it appeared that in the present state of knowledge it was better that these insects should be monographed by genera or families rather than on a geographical basis. It is at least certain that, had we dealt with them in a necessarily imperfect manner, no general conclusions could have been drawn from the work. The parasitic Hymenoptera collected by ourselves have been presented to the British Museum; those collected by the workers from Honolulu, and this is the greater part of the material, are in the Bishop Museum.

The Census

The total number of species of insects dealt with in this work is 1,603. In this figure are included not only the 1,568 species, specimens of which occurred in the collections under consideration, but also 35 others which are definitely

* The term is convenient if not scientific.

† Holdhaus (1934) observes, with justice, that the number of beetles recorded from Samoa is under 400, but that an expert collector spending some years in the islands, and devoting due attention to the insects of the soil, might raise the figure to 1,500 or 2,000.

‡ For example, no Japygid is recorded in this work. But Silvestri stopped a few hours in Pago Pago and collected the type of a new species (Silvestri, 1930).

recorded in earlier papers but not represented in these collections. In addition to the above, a few species have been mentioned by authors in the text, on the ground that they will eventually be found to occur in Samoa ; there are also 39 which have been referred to a genus, the specific identity being left uncertain ; the species which fall in both these categories are additional to the total of 1,603 species, which are definitely and precisely known to form a part of the insect fauna of Samoa.

A table, showing the number of Samoan species in each order of insects, and the number and percentage at present supposed to be endemic, is given on page 67 below.

The number of new insect genera described in this work is 80. The number of new species is 669 ; in this total we have not included a few species collected from Tonga, etc., but not from Samoa, and described in this work because they were closely related to Samoan insects.

With regard to the terrestrial Arthropoda other than insects, a total of 113 species is dealt with in the text, but it must be remembered that no collection of mites (Acarina) was made. Of this total 52 were apparently endemic. There were 15 new species and one new genus among them.

As a result of this labour in the field and the museum, it may be stated with confidence that the insects of Samoa are better known than those of any group of islands in Melanesia or tropical Polynesia, excluding the Hawaiian Islands. Extensive collections have also been made in the Marquesas, and a short review of the insects has appeared (Mumford and Adamson, 1934) ; a more comprehensive report on it is awaited with great interest. Though our knowledge of many groups of Samoan insects is still very imperfect (page 37), the collections on which the *Insects of Samoa* is based have resulted in a very great increase in knowledge. This is evident when it is seen that 1,603 insects are known to occur in Samoa, of which 669 are described as new in the present work. Even in the Orthoptera, which were carefully collected by Rechinger (Holdhaus, 1908), the total number of Samoan species has been raised from 48 to 78. The weevils (Curculionidae) had also been previously investigated : Marshall's * earlier

* In referring to work published in the *Insects of Samoa*, I have generally thought it sufficient to say " Marshall states " or " Edwards holds the view that," and to give no further reference. But when it seems necessary the distinction is made between an author's paper published elsewhere (Marshall (1921) in the present instance) and his contribution to this work (iv, 249, referring to part iv, p. 249).

paper (1921) included 22 species (15 genera), and his contribution published in this work (iv, 249) deals with 86 species, which belong to 55 genera. The increase in our knowledge of Fulgoroids is similar: Muir (1921) dealt with 26 species which belonged to 19 genera: the same author has now (ii, 1) made a list of 51 species and 27 genera. There are other groups, previously almost unknown. We now know 103 Samoan Heteroptera, instead of 6 *; 137 Microlepidoptera instead of 6; 36 Scolytidae instead of one; and 100 Nematocera of 9 families instead of 11 of 2 families.

II. THE INSECT FAUNA: ITS PECULIARITIES AND CHARACTERISTICS

Biological Notes

General.—If we wish to think of the Samoan insects in their natural environment, we must bear in mind the considerable body of information which has been set out in an earlier part of this work (ix, 1–19). Briefly, we may say that Samoa lies within the tropics, and that the islands are steep and volcanic. There is a sharp distinction between the forest-covered hills and the coastal belt, which is less rough and in many places cultivated. The climate is warm, moist and uniform, and this is true of every part of the archipelago. Two climatic events show some seasonal difference; there is a time of heavy rain; also there are considerable differences in insolation, though the influence of this upon the temperature of the air is masked by the thermostatic effect of the ocean. The mountain forest is luxuriant, and epiphytic plants and Cryptograms are abundant: a high proportion of the flora is endemic. The fauna, apart from insects, is limited, and many groups are totally absent: the proportion of endemic forms is high. The people are probably Asiatic in origin. In the old days they made use of a great variety of plants which they must have carried about the Pacific on their remarkable voyages, and doubtless they carried a number of small animals. The influence of European shipping has been felt

* The figure is given as 5 by China (ii, 81). Since his paper was published he has called my attention to an additional Reduviid, *Adricomius annulatus* described from Samoa by Distant (*Ann. Ent. Soc. Belg.*, vol. 47, pp. 60–61, 1903).

for a little more than a century, and a number of recently introduced plants and insects flourish.

In this home the collectors obtained 1,603 species of insects, of which 787 appear to be endemic to Samoa. It would perhaps be fair to say that the majority of these forms of life exist in a rather generalized environment. By this I mean that they live and breed in dead moist leaves, or in rotten wood or in soil.

Collecting in the hills, one does not easily realize the abundance of insects which occur ; indeed Scott's (1933) description of the insect life of the Seychelles would be almost true of Samoa. One walks along a path through the forest, but sees very few insects, even if one sweeps the herbage. But by devoting attention to a particular tuft of ferns on a tree trunk, or to a mass of the climbing Pandanid, *Freycinetia*, one discovers a number of minute Psocids, Tineina and sometimes Fulgoroids. Rotten trunks of different sorts of trees certainly have their particular fauna of Scolytid and other beetles. Our rather short stay in Samoa did not enable us to acquire knowledge of the particular environmental niches which are occupied by the native insects ; a glance through the pages of the present work will reveal how little is known, in comparison with the records which Perkins accumulated in Hawaiia. The matter is commended to those who may be able to give it the attention it deserves.

Collecting at night, particularly on the verandah at Malololelei, did not often produce large numbers of insects. There is, however, one night which stands out in the memory, that of 24th February, 1924 ; on this occasion I collected 350 moths out of perhaps ten times as many on the verandah, and noticed the relative scarcity of insects of other orders. There were a dozen Cerambycids, and a few Scolytids, all apparently of one species ; there was also one Pentatomid and three Cicadids (*Baeturia exhausta*) ; besides these there were hundreds of Tipulidae (*Trentepohlia*).

Effects of Season.—In making our collections, Hopkins and I started with the knowledge that we were at work in a tropical archipelago with an equable climate ; we wondered whether we should find seasonal forms of insects, or any evidence of prevalence at particular times of year. With regard to seasonal forms, one may say at once that no author has observed them ; even Prout, after examining a series of 260 *Cleora samoana* taken in every month of the year, concluded that there was no relation between the season and the occurrence of any form of this extremely variable moth. Among the butterflies there are one or two species which have " dry " and " wet " forms in other parts of their

distribution, but in Samoa they are consistently "wet": *Melanitis leda solandra* * is the clearest example of this.

As to evidence of seasonal prevalence of particular species, little is yet known. From what has been said of the climate (ix, 10–19), it might be expected that most of the insects would be active throughout the year, and this is generally true; Chopard, for instance, has remarked upon it in discussing the Orthoptera. But it is known that some at least of the trees flower at particular times of year (ix, 25), and we may suppose that this determines a seasonal prevalence of the insects which are dependent upon them for pollen, or nectar, or fruit. The only clear case of seasonal prevalence which has yet been noticed is in the butterfly *Precis villida samoënsis;* in the year 1924 Hopkins noticed that this butterfly was common in Apia from September till December, and that it was rare in the other months. In 1925 we gave particular attention to the matter, and the same seasonal prevalence was again apparent. On our occasional visits to Aleipata, at the east end of Upolu, or to Savaii, we found the butterfly abundant at the same time of year. These facts cannot be explained; the feeding habits are not known.

Our principal task in Samoa was the detailed study of the biology of a mosquito, *Aëdes variegatus*, which is of considerable importance as the vector of the local filarial diseases of man. This insect lays its eggs in small rot-holes, half coconut shells, and similar places, and in order to understand why these places were chosen we carried out an extensive series of experiments with trap breeding places. We found, among other things, that continuous heavy rain reduces the number of eggs laid in the traps, and that dry spells of two or three weeks had a still greater effect (Buxton and Hopkins, 1927). These differences in the size of the population of this insect may perhaps be called seasonal, depending as they do on climatic events, but it is to be understood that they are not of regular occurrence.

In the systematic parts of this work care has been taken to publish the dates on which specimens were captured. We do not yet know whether many of the insects have seasons of prevalence or not, but we are confident that our facts will be of value to some one who may care to inquire further into the matter.

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* So referred to by Hopkins. Poulton and Riley (1928) refer specimens from the Society Islands and Tonga to this form, and remark that all their specimens are of the wet-season form. They find consistent peculiarities in Samoan material, which they refer to a new subspecies, *M. l. hopkinsi.*

Effects of Altitude.—In considering range in altitude, we must remember that if an insect extends its range from the coast to the hills, it will reach a lower temperature and also, according to Angenheister (1924), a greater daily range of temperature ; it will also be exposed to more rain (ix, 17). On the other hand, it will escape from many introduced weeds and other plants, and from some of the introduced animals. As conditions are so different, it is not to be wondered at that the greater part of the Samoan insects have been collected either in the hills, for instance at Malololelei, or else near the coast ; the proportion of species which have been found in both is low. But as the facts are all accessible in the systematic Parts of this work, it seems unnecessary to quote examples. Hopkins mentions an interesting example of distribution limited by some factor unknown. The butterfly, *Issoria sinha bowdenia*, was found in all the Samoan Islands, and it was common throughout the year in the coastal region. But it was never seen above 1,000 feet, though its food-plant, a small native tree, grew up to 2,000 feet. The limitation of the insect to the lower levels cannot be due to the distribution of its food ; it is not easy to ascribe it to the action of imported enemies (which would readily explain a reverse distribution, with absence from the low ground) ; and it is not probably due to temperature, for the same race of the insect occurs in Tonga, which is a good deal cooler than Samoa.

Effects of Wind.—It will be remembered (ix, 18) that winds in Samoa tend to blow from the east or south-east at all times of year, and that for months on end they are very steady ; this regular south-easterly wind is the trade wind. The surface drift of the ocean is from the same quarter. It therefore seems that we are confronted with an anomaly, for the flora and fauna is unquestionably derived from the west but winds and currents come up from the east or south-east. But the difficulty is not so great as it seems to be, for it has been shown (Thomson, 1925) that the trade winds are shallow—no more than 2 to $4\frac{1}{2}$ miles deep ; over them lies a much greater stream of air, the anti-trade, which generally blows at a greater velocity than the trades ; its direction is approximately opposite to that of the trade wind. Neither can we forget the hurricanes, or cyclones : Visher (1925) has pointed out that these winds strip leaves and branches from the trees, and may therefore introduce living things into the upper air. They also produce occasional floods, so that rafts of vegetation, following a hurricane, may drift far out to sea. Even though hurricanes are rare in Samoa, they are common enough a few degrees to the west, and it is possible that forms of life, swept up in Melanesia, have occasionally landed in Samoa.

The carriage of insects over great distances by wind, and in particular by the currents of the upper air, may be of great importance ; it is now becoming possible to investigate it, and a considerable body of fact already exists. It is, of course, well known that insects, including many whose powers of flight are limited, circulate in the wind near the ground ; Fulton and Chamberlin (1931) have described traps which operate 20 to 30 feet above the ground, and which catch large numbers of small Homoptera, flies, moths, beetles, etc. ; Ball's (1918) records of the insects which reach the lighthouse on the Rebecca Shoals 105 miles from Florida are well known. But it is easy to see that if insects are circulating over the face of the earth, they may easily be carried upwards, perhaps by convection currents (an agency which would not be easily detected by the ordinary methods of meteorology, though the modern sport of gliding tends to call our attention to them). Moreover, we have a few actual records of insects collected at altitudes of a few thousand feet : applied entomologists have begun to use trapping devices attached to aeroplanes, and a large number of minute insects have been collected at these heights. Coad (1931), for instance, describes an apparatus which can be brought into use at any time during a flight, so that the level at which the insects actually occurred can be known. Within 2,000–3,000 feet of the ground, a great variety of insects may be found, including moths and other insects of strong flight. Higher up—and the investigators (and the insects) penetrated to 14,000 feet—the insects were nearly all small and weak, and many wingless forms were taken *. A number of other records of insects which are distributed by wind, and a general discussion of the subject, is given by Felt (1928) : he calls attention to the fact that the winds of the upper air are swift and very constant in direction.

To me it appears that a number of facts about Samoan insects can best be explained by supposing that they have reached the islands through the upper air. One can mention a number of minute insects, found in Samoa and in other places very far away. The Ceratopogonid, *Forcipomyia ingrami*, occurs in Fiji, Samoa and West Africa ; *F. inornatipennis*, a common West African species, has been recently recorded from the Society Islands (Macfie, 1933) ; several of the Samoan Psychodidae are apparently almost cosmopolitan. The mosquito, *Aëdes vexans*, occurs in the Palaearctic and Nearctic Regions, including many

* A very recent paper by Berland (*Ann. Soc. ent. France*, Vol. 104, pp. 73–96, 1935) should also be consulted. The author, working in France from an aeroplane, has collected a variety of small insects, some of them alive, up to 2,300 metres.

places which are quite cold ; it is also known from a number of parts of Asia, and it extends eastwards as far as Samoa ; it is even known to occur on some Polynesian atolls. Wherever it occurs it tends to breed in shallow, temporary pools, and to disappear from a locality after existing for a generation or two ; there is no reason for thinking that it is introduced by man, and it seems likely that it owes its wide and erratic distribution to winds. Edwards has called attention to the fact that the Samoan Nematocera tend to be small and light, and that the larger Bibionidae and Tipulidae are absent.* This again seems to point to aerial distribution.

The examples quoted are all Diptera, but examples from other groups of insects can be mentioned : for instance, the Collembolan, *Onychiurus fimetarius*, is known from Europe, North America, Africa and Sumatra, as well as Samoa ; but as it occurs in soil, it perhaps owes its distribution to some factor other than wind. Osborn records several minute Cicadellidae previously known from India or Ceylon : but whether spread with food-plants or by wind who can say ? The small Zygopterid dragon-fly, *Ischnura aurora*, is clearly an insect which owes its very wide distribution to carriage in the upper air ; Fraser himself has seen the newly emerged insects rise high into the air until they were lost to sight, and it seems that its very weakness has allowed this insect to spread not only from India to Samoa, but even out to the barren atolls of the Ellice group (vii, 23) and the Tuamotu Archipelago (Cheesman, 1927).

There are also several minute Coleoptera, the distribution of which may perhaps be due to wind, though a more intimate knowledge of their biology is desirable. The minute (1·3 mm.) Anthribid, *Scirtetinus pacificus*, endemic to Samoa, but congeneric with species found only in the Seychelles, may be wind-borne : compare also the Scolytidae known only from Samoa and Ceylon, especially *Scolytomimus*, a genus containing only two species, one endemic in each island ; also the small (2 mm.) Colydiid, *Hystricones vagans*, of Samoa, representing a genus of which the only other species is Central American. It is interesting to see that Scott (1933, p. 328) records several species of minute beetles, of different families, each one known only from the Seychelles and some remote island (Hawaiia in two instances).

It is possible that the distribution of these beetles and other insects may be more normal than it appears to be : further research may show that they occur

* And compare Edwards' (1926a) observation that in the Philippines the large Tipulids tend to have a restricted distribution, the smaller Limnobiidae to be more widely spread.

in many intermediate countries : the fact that they seem to be confined to islands may be due to the care of individual collectors, or because obscure and minute forms are more readily discovered in a limited fauna. But to me it seems probable that they have been distributed by wind, particularly by the currents of the upper air, and that it is to their minute size that they owe their immense, rather erratic, distribution.

But we must admit that there are certain groups which seem not to have been distributed by wind, though they are small. The fact that all the Aphids, and nearly all the Coccids, belong to species of wide distribution may perhaps be due in part to wind-dispersion, though many of the species are pests of introduced agricultural plants, brought in by Europeans. If carriage by wind had been effective in the case of these insects, we should surely have expected to find endemic species descended from those which arrived in the remote past. The complete absence of native plume moths, Pterophoridae (ix, 67), which seem so well adapted to wind carriage, is also most remarkable.

It appears that the distribution of spiders in Samoa and other remote islands may perhaps give evidence of carriage by wind, for it is familiar that young spiders of many sorts throw out gossamer by which they are carried high into the air. It will be remembered that the Samoan spiders are rather well known, and that of 81 species, 46 are endemic and 25 are found elsewhere in the Pacific, one or two of them extending so far as New Caledonia and the Malay Islands. The remaining 10 are cosmopolites, many of them of recent introduction. The 71 species which may be presumed to be native are most unevenly distributed among the families, for there are no Mygalomorphs or Drassidae, and certain other families are very slightly represented. In these particulars, there is general resemblance between the spider fauna of Samoa and of the Hawaiian Islands. The Samoan spiders were dealt with by Berland (viii, 38), and the same author (1934a and b) has discussed our present knowledge of the spiders of the Pacific region. It appears that the Mygalomorphs are known to occur in all the lands which form the western border of Oceania, the Philippines, Japan, the New Hebrides, Loyalty Islands, New Caledonia and New Zealand : and that they extend eastwards to Fiji, where two small species occur ; but there are none in the archipelagos farther to the east. It might therefore be said that the Mygalomorphs have a continental distribution. Berland (1926) has also discussed the species which possess a wide tropical distribution. He is of opinion that all these owe their spread to human agency, though it is not neces-

sarily recent, and that carriage by air has had little to do with the geographical distribution of spiders. He holds that, inasmuch as the spiders of islands are largely endemic, and since there is a great difference between the spiders of Madagascar and Africa, distribution as aeronauts cannot be effective.

The matter has also been studied by Bristowe, who has published a general account of the distribution and dispersal of spiders, considering the effects of various climatic factors including wind, also of soil, plants and human activities (Bristowe, 1930). He has also collected on Krakatau and discussed its spiders and the method by which they may be supposed to have re-colonized it since the eruption of 1883, which is believed to have sterilized that island completely (Bristowe, 1931). Bristowe does not question the importance of human agency in distributing spiders, and it is clear that certain species which are widely spread are domestic. But he clearly holds that distribution by air also occurs, and that it is important. He finds little difficulty in meeting Berland's objections to this view, and produces a large body of evidence which appears to show convincingly that dispersal by air is common and that it explains much of the geographical distribution of spiders. In particular, he discusses the absence of Mygalomorphs, Drassidae and Tetrasticta from Samoa, Hawaiia and other islands, and he makes it appear probable that their absence is due to the fact that the young spiders produce no threads and are not aeronauts.

It is hardly possible to express an opinion on a matter which has proved puzzling to experts, but Bristowe's view appears to be founded on a large body of fact, and it provides an explanation of what is characteristic of the spiders of Samoa and many other archipelagos.

Lack of wings, or of power to use them, is characteristic of insects inhabiting certain islands. But I know of no evidence that this is so among Samoan insects : I think that none of the systematists has discovered a high proportion of apterous forms in his material. In one or two groups it is certain that there is not a high proportion of wingless forms ; for instance there are about six native Blattidae, all of them winged ; in the Gryllidae there are 32 native species, of which 20 are winged, the remainder wingless (but two of these have winged males, wingless females). The matter is mentioned here, for it is generally held that it is the exposure to wind which causes insects on certain islands to be apterous.

Migrant Insects.—At this point it is appropriate to consider the migrant insects, though it is not certain that their distribution or flight have any relation to wind.

Among the butterflies, the most interesting is *Danaida archippus;* its history in Samoa is dealt with by Hopkins (iii, 7), and the story of its spread in Oceania is known in detail, thanks to Walker (1914), Collenette (1925a), and Poulton and Riley (1928). It is remarkable that it occurs on a number of the smallest and most remote islands, including the barren atolls of the Ellice group. A general account of its flights in America and elsewhere is given by Williams (1930, pp. 141–156). So far as Samoa is concerned, the only known food-plant is the weed, *Asclepias curassavica*, which must owe its introduction to European shipping, and may well have come in as seed, with hay or straw. But the butterfly could not have reached Samoa in dry material, at any stage of its existence, and we must suppose that it came by flying. But if its distribution is by flight and if it feeds only on a plant of recent introduction, then members of this species must have been flying about the Pacific, seeking to colonize the islands, for countless ages. The earliest record of the butterfly in Samoa is in 1869. A record which is similar in certain respects is given by Wood-Jones (1910, p. 352); the moth, *Plusia chalcites*, a notorious migrant, was apparently absent from Cocos-Keeling, until tomatoes were grown, when it appeared on the plants: the tomato seed came by post from England, so that one can be confident that the insect was not introduced in that way. The conclusion to which Wood-Jones came is that the moth arrived by flight, and established itself because the tomatoes were growing: inasmuch as it arrived soon after the plants began to be grown, it seemed highly probable that it had repeatedly reached Cocos-Keeling, but failed to establish itself.

There is some evidence which suggests that another Danaine butterfly, *Hypolimnas bolina*, owes its distribution in the Pacific to recent flights from island to island. It was apparently absent from Pitcairn Island in 1883, but it has been recently found there (Poulton and Riley, 1928)*; it is improbable that it had been introduced in one of the early stages on living plants. But, as to Samoa, we may be certain that this butterfly is not of recent arrival, for it has developed peculiar forms, which are different on different islands in that archipelago, though they are not confined to Samoa.

Among the moths the following Samoan species are known to be migrant, at least in some part of their range: *Herse convolvuli*, *Hippotion celerio*, *Heliothis*

* Poulton and Riley's paper states that they have examined specimens received from Mr. C. J. Grist, but they do not quote the date of collection. Mr. Grist has since informed Prof. Poulton that the specimens were collected in 1923 and subsequent years.

armigera, *Prodenia litura* and *Plutella maculipennis*.* But all these insects are known to feed on many sorts of plants, including economic plants of which they are frequently pests : it seems impossible, therefore, to discover how much of their range is due to flight and how much to artificial introduction. *Achaea janata* falls in the same group. It is known to be a pest of many crops (iii, 175), and may owe its occurrence in Samoa, and its wide distribution in the tropics of the Old World and in Polynesia, to artificial introduction. On the other hand, there is a record (under the name *A. melicerta*) of a single specimen flying aboard a yacht 450 miles from Ducie Island and much farther from any large island (Collenette, 1925b). It is possible that the wide-ranging Arctiid, *Utetheisa pulchelloides*, is a migrant, as the nearly related *U. pulchella* is known to be.

On the other hand, there are several notorious migrant Lepidoptera which are not known to occur in Samoa. The small moth, *Nomophila noctuella*, was not found, and it appears that it is not known from Fiji and Tonga ; this is remarkable, for it is very nearly cosmopolitan, and it occurs in the Malay Islands, Formosa, Australia and Hawaiia (W. H. T. Tams, by letter). The absence of " Painted Lady " butterflies (*Vanessa cardui*) is also remarkable, as there is an endemic race of this insect in Australia, Tasmania and New Zealand (*V.c. kershawi*). There is a record of the capture of one specimen of this race in very worn condition at Suva, Fiji (Williams, 1930, p. 204) ; in coming from its breeding place it must have crossed about 1,000 miles of ocean, but in spite of this individual occurrence, the species has failed to establish itself in Oceania.

It seems certain that the majority of migrant insects in the Samoan fauna are Lepidoptera, but it is probable that several of the large dragon-flies (Anisoptera) are also migrants, though I do not think that any records of actual movement have been observed in Samoa. Among them it is probable that *Diplacodes bipunctata*, *Tramea limbata* and *Pantala flavescens* reached the islands from time to time as active migrants : it is quite likely also that representatives of *Anax*, *Hemicordulia*, *Lathrecista* and *Orthetrum*, all of them widely distributed in the tropics, fall in the same group. Fraser, indeed, has put forward the view that all the Samoan Anisoptera are migrants with the exception of three endemic species of *Hemicordulia* and *Gynacantha*. The interesting Zygopteron, *Ischnura aurora*, which appears to have been distributed by air currents rather than actively as a migrant, has already been discussed (p. 44).

* This insect was certainly present in Samoa, and material was collected. The specimens seem to have been lost, and they were not included in the collection dealt with by Meyrick.

Insects of Special Environments.—In Samoa we collected in a few places of particular interest; it is clear that the highly specialized creatures which inhabit these spots must have encountered particular obstacles in reaching their present homes; these would not have been entirely avoided had they possessed the power of calling land-bridges from the vasty deep. The particular environments which we shall describe shortly are mountain gullies, lowland swamps, mangroves, the strand and the caves.

(1) Mountain Gullies.—The steep mountains of Samoa, which receive such abundant rain, are scored by innumerable parallel gullies, the sides of which are often nearly vertical; the water in these gullies rushes down in a series of rapids and waterfalls (ix, 5–8). At Malololelei, Upolu, it was easy to collect insects in two of these ravines; at this point one was about 2,000 feet above sea-level, and near the heads of the streams. The type of scenery and vegetation is shown in Plates I to III, and V and VI (Part ix). A very similar environment exists even as low as Vailima (600 feet), though here the streams tend to be larger. One might indeed say that forest full of ravines and rapids is typical of nearly all parts of Samoa, except the actual coast, and a zone of a few hundred feet above it.

On the bank of such a stream, often on a patch of wet sand, one would find the little grasshopper, *Paratettix compactus*. In the stream itself were great black boulders of basalt; on the down-stream side of a boulder, close to the water, *Anaxipha hopkinsi*, an endemic cricket, used to sit. Owing to its colour it was most difficult to collect it, especially as it flies freely and can jump to the surface of the rushing water upon which it swims easily. We noticed that this insect seemed to be confined to the boulders which stood in the water; it was not found on those on the bank, even when the stream was no more than a dozen yards across. Another interesting insect, almost equally specialized in its habit, is the Anthomyid fly *Limnophora immaculiventris*; this fly selects a place where the surface of the torrent is relatively still, under the protection of a mass of rock, and there it skates over the surface of the water. It is difficult to see, and even more difficult to catch, and it may easily be mistaken for one of the Gerrid or Veliid bugs which have the same habit. Nothing is known of the breeding place of this fly, but it is understood that most members of the genus are associated with water.

The most interesting insects which may be found in the ravines near Malololelei are the Ischnuran dragon-flies. Eight members of this group are at present

known to exist in Samoa. *Ischnura aurora* has an enormous tropical dispersion, and does not at the moment concern us (see p. 44, above). But of the remaining 7 species, 4 (*I. buxtoni*, *I. haemastigma*, *Amorphostigma auricolor*, *Pacificagrion lacrimosa*) have never been collected except in one gully at Malololelei ; one (*A. armstrongi*) is known from that gully, and from another place in the hills of the same island ; one (*I. albistigma*) has been collected in the same gully and also in Tutuila ; one species (*I. chromostigma*) is known only from a place in Tutuila. When the innumerable other gullies in the Samoan forests are explored, it may be that the seemingly extreme localization of these insects will disappear, and that they will be found widely dispersed in one or several islands. But it is at least possible that the group of species collected by Armstrong and others in the one gully is only a small sample of the Ischnuran fauna of Samoa. The Samoan Ischnurans form an interesting parallel to the dragon-flies of the genus *Nesobasis* in Fiji, though I understand that *Ischnura* is not closely related to *Nesobasis* apart from the fact that they are both Agrionids. According to Tillyard (1924) the genus *Nesobasis* is at present thought to be confined to Fiji, save for the existence of a species on Bivak Island, S.W. New Guinea. From Fiji 13 species are already known, of which 10 were collected by Simmonds along the Waidoi River, Viti Levu ; it is not recorded whether the 10 species occurred together, or whether they were localized in different parts of the river's course. Here again, we do not know whether further search on Viti Levu, and elsewhere in Fiji, will show that these species have a relatively wide distribution, or whether enormous numbers of endemic and highly localized species remain to be revealed.

In these gullies and in other dark places in the forest one may find that curious complex of Tipulids and Pholcid spiders, more fully described elsewhere (vi, 95). The Tipulids (*Trentepohlia* spp.) are extremely abundant, congregating in large numbers among buttress roots or under overhanging rocks ; here they stand swaying on their long legs. The Pholcids (*Pholcus* and *Smeringopus*) sway in a similar manner on their webs in places of the same type, and their legs have pale joints which resemble those of the Tipulids. The resemblance was noticeable in the field. In the same places we occasionally got a Reduviid (*Gardena*) shaped almost like a Tipulid with a very slender body and long legs, but it was so rare that we have no knowledge of its habits.

At least two groups of insects, which one might have expected to find in the torrents and waterfalls, were apparently absent ; I refer to flies of the families

Simuliidae and Blepharoceridae, the early stages of which are so often associated with water of this type. The absence of Simuliids is particularly curious, for these insects occur farther to the east in Tahiti and the Marquesas (p. 87).

One can hardly think of the insects found in torrents without wondering whether similar evidence might be derived from specialized plants; but this is not the case, for the Director of the Royal Botanic Gardens, Kew, tells me that there are two families of higher plants, the Podestemonaceae and Tristichaceae, which are characteristic of torrents in the tropics; neither occurs farther east than Java, and no help can therefore be derived from them.

(2) Lowland Swamps.—In contrast to the torrential mountain streams are the coastal swamps, in which the water moves slowly, though it is not generally stagnant. These occur in many places, and we collected in them at Apia, Laulii, Mulifanua and elsewhere. The great majority of these swamps have been enlarged and cleared by the Samoans, who grow taro in them. The characteristic dragon-flies are the large Anisoptera, the majority of which have an enormous range in the tropics of the Old World. The species of Dytiscidae which were obtained in these swamps were also of wide distribution; the same is true of the Gelastocorid, and of one of the Notonectids. There were also a few Chironomidae, but Edwards remarks on the paucity of the water-breeding Nematocera, compared with those which breed in rotten wood or leaves. One interesting Culicid is found, *Aëdes kochi samoana;* this insect breeds almost exclusively in the axils of the taro plant, *Colocasia*, which is planted in these swamps. From what has been said it will be seen that the fauna of the coastal swamps has not provided much of interest; I fear that it may have been still further reduced by our successful introduction of a "top minnow," *Poecilia sphenops*, from Panama.

(3) Mangroves.—At the places where the rivers and streams eventually reach the sea, some of them have small muddy estuaries, overgrown with mangroves. The fauna of a mangrove swamp, which is exposed alternately to salt and fresh water as the tide rises and falls, is not rich, and is mostly marine; but in the mangrove trees one finds a few insects, *Aëdes variegatus* breeding in profusion in holes and cavities in the trunks, and the small, endemic, cricket *Apteronemobius longipes*, running on the trunks and hiding in little cavities; this particular insect was never found except among mangroves, on which its dark colour makes it difficult to detect. It is wingless, but covered with fine hairs, which prevent it being wetted (even by alcohol), and it swims well though

it does not appear to take readily to water. When the tide is out the crickets descend from the trees and run about on the black mud among crabs, gobies and other marine creatures.

(4) The Strand.—But most of the shores of Samoa are not fringed with mangroves. There are very many sandy bays, separated from one another by rocky headlands. The white sand, which is really pounded coral and shell, is crossed by long strands of *Ipomoea* and one or two Leguminous creepers. There are also a few trees and bushes in this "strand vegetation," all of them very widely distributed in the Pacific and Indian Oceans, and strictly limited to this littoral zone (Guppy, 1906; Setchell, 1924, p. 15). Many of the plants have widely distributed insects associated with them. Thus the yellow creeper *Vigna lutea* (*marina*) is the food-plant of the Lycaenid, *Jamides argentina*, the Samoan representative of the widely spread Indo-Malayan *J. bochus* (iii, 52).

One of the most characteristic of the trees is *Tournefortia argentea* (Boraginaceae). This tree was the food-plant of the Arctiid, *Utetheisa pulchelloides*: the same insect has been recorded as feeding on this tree in the Tuamotus (Collenette, 1928) and even in certain remote coral islands, Chagos, Amirantes, etc., in the western Indian Ocean (Scott, 1933, p. 338 footnote). This widespread association of plant and insect is interesting, but it tells us nothing of the means by which the moth reached the many isolated spots in which it is now found. We suggest above (p. 48), that it is probably a migrant, but it seems clear that tropicopolitan insects, associated with strand plants, deserve much more experimental study than they have received: in particular we desire to know whether there is any stage at which they resist sea water, and whether the egg stage is ever so prolonged as to permit the insect to travel on drift wood. The insects of the strand appear unattractive, for they are so widely distributed, but they are every bit as interesting as the strand plants which were the object of the researches of Guppy. That author showed long ago (Guppy, 1906) that *Tournefortia argentea* has a vast Indo-Pacific distribution, occurring on the strand of the smallest and most isolated islands; that the small seeds have a coating of buoyant corky material; that they are common in drift material; and that they will float for a year in sea water. Hopkins has described the aggregation of large numbers of males of the butterfly *Euploea s. schmeltzi* round dead or withering branches and fruit of *Tournefortia argentea*. A similar habit has been observed in many other species of *Euploea* in a number of different parts of the Pacific (for references see Hopkins, iii, 15; also Lever, 1934; Buxton, 1927;

Poulton, 1932). In each place it is males only which are attracted, and where several species occur on the same island they may all be seen together; it is only the dead and withered parts of this particular tree which are visited; the visits are observed by day; assembling for sleep at night, as so many species of *Euploea* do, is a distinct habit. The suggestion has been made by Hopkins that dead pieces of *Tournefortia* may give out an odour which resembles that of the female butterfly. It is not easy to prove or disprove the suggestion, but it would be of interest to test whether an infusion is also attractive, and whether the boughs remain attractive if concealed with muslin.

(5) Caves.—Another specialized environment is the cave, of which a number exist, though only that near Malololelei was visited. It will be remembered (ix, 7; Plate IV, B) that this cave is a lava tunnel, and that one can penetrate it for about 200 yards; it is relatively straight, and a stream enters it at the upper end, but later runs beneath the floor, so that from that point the cave is much less wet. The temperature inside the cave in May was 22·5° C., and one may assume that there is very little variation from this figure throughout the year. As the cave is generally straight, and as the stream runs into it, one would expect to find animals which do not in any sense belong to the real cave fauna; in this group we should probably put a dragon-fly (*Hemicordulia* sp.) which visited our lanterns on one occasion, also several undetermined spiders which were found at the far end of the cave, and the Atyid prawns (*Caridina*) which were common in the stream, both outside and also inside the cave even in total darkness.

Bats and swifts form an important part of the fauna of the cave. The only species of bat (*Emballonura semicaudata*) is a small insectivorous one, hundreds of which live in the cave, especially in the more remote part, at all times of year. They were infested by the Streblid, *Nycteribosca buxtoni*. The swifts (*Collocalia spodopygia*) are an endemic Samoan species; they construct minute nests of moss and liverwort on shelves upon the walls of the cave; we were surprised to find them breeding even at the far end of the cave, in spots which were totally dark. It appeared that these birds haunted the cave at all times of year. In spite of the fact that we collected a considerable number, we obtained no parasites from them.

These two vertebrates, which live in the cave and feed in the forest, bring in considerable quantities of material. We made no search in the nests of the swifts, but the large heaps of bats' dung, which accumulate on the floor of the

cave wherever it is not covered by the stream, provided interesting material. In it we found larvae of a fly, of which we failed to breed adults; in the same place we discovered the Pseudoscorpion, *Chelifer buxtoni*. On the heaps of bats' dung one could always find specimens of a most interesting Locustid, *Rhaphidophora rechingeri*. These are insects of amazing agility, and it is not easy to catch them by lantern light, as they leap about among boulders and heaps of bats' dung; even when they fall into water, they are capable of swimming across the surface. This insect was described by Holdhaus (1908), from material which Rechinger collected in Upolu and Savaii; Holdhaus gives no notes on biology and no precise locality. The species is believed to be endemic to Samoa, and its existence raises two very interesting questions. The first of these is biological: *R. rechingeri* lives, so far as we know, only in a cave, but if it left the cave it could find most of the necessary conditions in the surrounding forests; it would find darkness and damp beneath stones and logs, or in heaps of fallen leaves, where many other creatures already live; if it requires an extremely equable temperature, this also exists in the forest.* In spite of this, we never found this insect outside the cave, and the Rhaphidophorinae are, in general, cave insects, in all the countries in which they occur. One might even say they are specialized cave-dwellers, lacking eyes and wings. On the other hand, I have a letter from Dr. R. J. Tillyard, in which he says:

"I have found that Rhaphidophorinae occur fairly commonly hidden under piles of loose rocks or stones in New Zealand, particularly in the stony beds of large, swift rivers, such as are common in New Zealand, and I think it highly probable that this is the more ancient habitat of the two, and that the cavernicolous habit has been assumed later. When, therefore, you say that the Samoan species has no other habit but that of living in caves, I can only reply that this is contrary to my general experience in New Zealand. It is true that many collectors in New Zealand would tell you that Cave Wetas only live in caves, but it is due to lack of observation on their part. Even the famous cave-dwelling genus *Pachyrhamma* is to be found sometimes under big, loose rocks; and, indeed, ecologically, one might ask, what *is* the difference, to an insect with a body one inch long, and hind legs and antennae both many times that length, between a true cave, and the large, irregular, dark interspaces between the tumbled rocks of a retreating glacier-face or the piled-up boulders in the bed

* It will be remembered that in the open garden at Malololelei, the mean daily range of shade temperature was 8° C., and in the edge of the forest, in a shelter hung in a tree, it was 4° C. One may assume that on the forest floor, among decaying vegetation, the range would be less, and that it might be immeasurable (ix, 15).

of a steep mountain torrent? Ecologically, I conceive that the cave is only the end-term of a series of habitats in which the factors of darkness and security increase in a sort of arithmetical progression."

This is Dr. Tillyard's experience in New Zealand, and it is possible that *R. rechingeri* might be found in the type of place which he describes, if search were made in Samoa; but I do not hold that this is probable, for we devoted particular attention to the Orthoptera, and were not unsuccessful in obtaining obscure Gryllids, etc. (i, 9–58). The second question, relating to this insect, arises from the first and relates to distribution. Numerous species of Rhaphidophorinae occur in New Zealand, and there are a few in Australia (Tillyard, 1926, p. 96). They also occur through the Malay Peninsula, and the islands as far east as New Guinea; none are yet recorded from Melanesia, Fiji or any part of Polynesia except Samoa (Karny, 1929), though perhaps their apparent absence from these archipelagos is due to our ignorance. But even if these insects are subsequently found in Melanesia and Fiji, and admitting that they are not absolutely confined to caves, their existence in Samoa is difficult to reconcile with the view that the fauna is "oceanic."

(6) Certain Parasitic Relationships.—Another type of specialist is the insect which is closely dependent on some other species of animal or plant. This dependence limits its distribution: for instance the Nycteribiid genus *Cyclopodia*, which is found in the fur of fruit-bats (*Pteropus*), occurs in Samoa, and presumably in Tonga, where these animals are found; but the absence of *Pteropus* from the Cook Islands, and the Society Group, must determine also the absence of the parasite. For a similar reason, as there are no wild mammals except bats and rats, Samoa contains none of the Hippoboscids which infest mammals. But this general relation does not always hold; for instance, the Hippoboscids found on birds are not specific. Ferris mentions that *Ornithoica promiscua* is found in California on Passerines and a falcon, and in the Philippine Islands on a woodpecker and a kingfisher; in Samoa it was collected from a fly-catcher and a heron. In a similar way, *Ornitheza metallica* has been collected in Samoa on a starling, and in the New Hebrides on a kingfisher; in Europe it has been found on the jay and the heron, and in the Philippine Islands on a bunting. It is clear that parasites such as these are heedless alike of the canons of systematic ornithology and of the "lines" of the zoögeographers.

Among other parasitic groups, one notices that the order Strepsiptera, and the Conopidae (Diptera), are not represented in the Samoan collections.

We may suppose that the conditions which allowed certain families of Hymenoptera to colonize Samoa did not let their parasites do so; it is clear that any random method of colonization which is perilous to a host species is much more so to a parasite, for it occurs in the body of no more than a small proportion of hosts. But the validity of this argument is weakened by the fact that two species of Pipunculidae are known to exist in Samoa. Enquiry along these lines might be extended. If, for instance, it were shown that gall-forming insects were rare, though common in the more "continental" islands to the west, the fact would support the view that Samoa is "oceanic." But the absence of facts relating to these insects and also the parasitic Hymenoptera precludes discussion at present.

Insects and Human Agency.—The endemic insects and other Arthropods are discussed below. It appears that of a total of 1,603 species of insects, 787 (49%) are peculiar to Samoa, so far as present knowledge goes. The remainder are either native, occurring in other countries, but having reached Samoa by natural means, or introduced, either by Polynesians or more recently by European ships.

It would be a matter of great interest could we divide all the insects into the three groups *endemic*, *native* and *introduced*, and at one time I attempted to do so. But I have now reached the conclusion that this is not possible, except perhaps for an expert in a particular group. It will be observed that Perkins (1913, p. xlii) discussed this grouping, originally suggested by Blackburn and Sharp (1885), but recognized the impossibility of placing many of the insects in the correct category. To me it appears best to distinguish only the endemic species from the others; this is done, for each order of Insects separately, in Table 1, p. 67. But though one cannot divide the whole of the Samoan insects into these categories, there are many individual cases in which this is possible. In certain circumstances one may go farther and show that it is extremely probable that introduction was due to the Polynesians, or alternatively that it is almost certainly recent and due to European shipping. For in dealing with the fauna of Oceania, one must never forget that the Polynesians made long and frequent voyages, and that they carried many useful plants with them (ix, 26). Let us therefore endeavour to distinguish the species spread by Polynesians from the more recent introductions for which the white man is responsible, and to distinguish both these *introduced* groups from the *native* fauna.

(1) Polynesian Introductions.—If an insect has a wide distribution in the Pacific, and is associated with a plant which was useful to the Polynesians in the days before the European arrived, one may assume that it was carried about in the canoes and class it as an early introduction. There are two excellent examples among the Fulgoroids: *Megamelus proserpina*, which feeds on the leaves of taro (*Colocasia*, Araceae) and is known to occur in northern Australia, many Malayan islands, Fiji and Niue *; and *Perkinsiella vitiensis*, which attacks sugar cane and is recorded from the New Hebrides (Muir, 1931, p. 72), Fiji, Samoa and Niue * (ii, 11). In the same group is the Aleyrodid, *Aleuroplatus samoanus*, described by Laing as endemic, but since found in Tahiti (Dozier, 1928); this insect feeds upon cultivated Croton (*Codiaeum*), a plant widely used in Polynesia and Melanesia for decorating graves and in other ritualistic practices. The relation of two Ortalidae, *Scholastes cinctus* and *bimaculatus*, to the life of Polynesians is rather different. These flies breed in the rotten meat of coconuts which have been cut for drinking while they were green, and the larvae can exist for many weeks without food if they consume all the rotten material in an unripe nut. They are therefore well suited for travelling the ocean with Polynesians. I may add that they do not breed in the kernel of ripe nuts, or in copra, so that their distribution cannot be related to European commerce. *Cassida strigula*, associated with an old food-plant, the sweet potato, may also be an ancient introduction, though Maulik attributes it to modern commerce: the same may be said of the sweet-potato weevil, *Cylas formicarius*. But one must be cautious of attributing all pests of old economic plants to human introduction; for instance, the hawk moth, *Hippotion celerio*, is a creature of enormous powers of flight and very wide range; it has many unrelated food-plants; and though it is a pest of taro in Samoa we may well think that it came to the archipelago by natural means.

These are also a few parasitic insects, of man himself or of animals which the early Samoans are known to have kept; in all probability these insects were brought to Samoa by canoe, though one must be cautious, for evidence suggests that bedbugs and human fleas were brought to these peaceful isles by the

* The occurrence of these insects in Niue is significant; this island is small and remote, and landing from ships is not easy; the island has no economic importance to the European, and is only visited a very few times in a year. This confirms the view that the insects are Polynesian introductions.

European. To native introduction one may perhaps attribute *Pediculus humanus* and *Phthirus pubis* of man; *Ctenocephalus felis*, a common parasite of dogs in the tropics; also three species of Mallophaga from domestic hens. I have already referrred to the pig-louse (vii, 86). At the time of writing it was held that the specimens belonged to a variety (*Haematopinus suis adventicius*) characteristic of the wild swine of south-eastern Asia. This appeared to give interesting and unexpected corroboration of the view that the Polynesians are derived from that area. But the recent and very careful investigations of Ferris (1933) show that *H. suis* is extremely variable, but lend no support to the theory.

In considering whether a particular insect is probably of recent introduction or not, one may sometimes gain assistance from the systematic position of its host plant. European food-plants are predominantly Cruciferae, Leguminosae or Gramineae, but the Samoans did not eat members of any of these three great Natural Orders. To this there is one apparent exception, for they grew sugar-cane, though mainly as a thatch plant. Pests of sugar, such as *Rhabdocnemis obscura*, may, therefore, have been introduced by the Polynesians or the European. But pests of stored cereals, for instance *Calandra oryzae*, are clearly due to European agency. So, in all probability, are the pests of growing bean plants, for instance *Maruca testulalis* and *Nacoleia diemenalis;* both these Pyraustine moths have a very wide distribution through India, Malaya and Melanesia, and attack growing Leguminous crops.

Furthermore, there are certain insects associated with the coconut, about which it is difficult to feel any certainty. There is, of course, no doubt that the palm was used and carried about by natives of Polynesia and Melanesia, indeed to many of them it was the staff of life. Moreover, they used it and carried it in a variety of states, for they drank from young green nuts, and used the ripe kernels, and they also ate the large spongy embryo inside nuts which had already sprouted: there were doubtless facilities for the carriage of insects as well as the plants. This is all well known, but we do not know whether the coconut is truly native of Samoa, having come floating over the sea and established itself before ever man reached the archipelago. For what it is worth, the evidence to be derived from insects suggests that coconuts are ancient natives of Oceania, as local endemic insects have developed, apparently, on this particular palm. For instance, there is a genus of Hispine beetles, *Promecotheca*, distributed through the Malay Islands and the Philippines to New Guinea, North Australia, Melanesia

and parts of Polynesia. A number of species are known, each one confined to a part of the area. The Samoan species (*P. reichei*), which is the most easterly in its range, is found in Fiji, Samoa and Tonga. All the species are attached to the one host plant, the coconut, except one from Zingiberaceae in the Solomon Islands. These facts appear to suggest that the palm is truly native in the islands mentioned above; were it only a cultivated plant, carried about by man, it would surely be attacked by a single, widely spread species of *Promecotheca* (for facts, see Maulik, iv, 210; also Maulik, 1929a and b). Another coconut insect is the Phasmid, *Graeffea crouani*, but it is of little value in the present discussion, because the systematics of the species which attack the coconut are obscure. Many other insects are known from coconut palms in Samoa, but the majority are probably of recent introduction (Laing, ii, 37; also Doane and Ferris (1916); also Swezey (1924)).

The insects of the banana and other plants might be studied in a similar manner.

The distribution of races of two species of *Aëdes* (Culicidae) shows anomalies which appear to be due to the voyages of the Polynesians; the cases are important, as we have so much knowledge about mosquitoes in Oceania. *Aëdes scutellaris* * is known to breed in small collections of water, including rain-water which has accumulated in a canoe, and its egg is resistant to drying. It has an enormous distribution in Indo-Malaya and also in Oceania, including many atolls; and it has developed a number of insular races, differing from one another both as adults and also as larvae.† In the area which is our concern, we find the typical form in New Guinea, the Bismarcks and the Solomons; var. *hebrideus* occurs in the New Hebrides, and probably in the small archipelagos to the north; var. *pseudoscutellaris* is known from Fiji ‡ and the Ellice group, and thence extends through Samoa to the Tuamotus, that is to say, to the eastern limit of Polynesia; the range of this last variety is partly interrupted by that of var.

* It appears that the insect referred to elsewhere in this work (vi, 44) as *Aëdes* (*Stegomyia*) *variegatus* Dol. must now be called *scutellaris*, Walker. The change is regrettable, for *scutellaris* Theo. is a synonym which has been used for a different species, *albopictus* (for synonymy see Edwards, 1932a).

† The distribution of the forms of this interesting insect and of *Aëdes kochi* was shown on maps by myself and Hopkins (1927); we also summarized what was known at the time of our publication, and gave a list of references. For recent additional information, see Paine and Edwards (1929); also Edwards (1929a).

‡ Specimens from Rotuma appear to combine the characters of this variety and of *hebrideus* (Edwards, 1929a, p. 338).

tongae, which occurs in Tonga, including the northerly outlying islands of the group. *Tongae* also occurs in the island of Sikiana, in the Solomon Islands, so that its range is interrupted by an interval of 1,500 miles, in which two other varieties (*pseudoscutellaris* and *hebrideus*) occur. This astonishing anomaly is, I think, explained by the fact that the Sikiana people are not related to other Solomon islanders, for they are purely Polynesian. There is evidence to support the view that, like the people of Tikopia and a few other islands on the easterly fringe of Melanesia, their ancestors drifted down wind from Polynesia and in their canoes they brought the Tongan race of this mosquito. It seems probable that the other races, and particularly var. *pseudoscutellaris*, owe their wide extension in the Pacific to carriage in native craft. The egg and the larva are well suited to such voyages, and until the European broke up Polynesian society there was much coming and going in great canoes which were capable of long ocean voyages.

In the same genus there is a second species, *Aëdes* (*Finlaya*) *kochi*, the distribution of which is probably partly due to human interference. Two forms of this insect are known, distinguishable in the adult, the larva and to some extent the breeding place ; the typical form is found in New Guinea, the Bismarck and the Solomon Islands ; it seems to be absent from the New Hebrides, where I searched for it on many islands, but it occurs again in Fiji ; in the Bismarcks it breeds in empty coconut shells, but in New Guinea, according to Taylor (1934b), it breeds almost exclusively in the axils of *Pandanus*, and occasionally taro (*Colocasia*). The variety *samoana* occurs in Samoa and Tonga. It breeds almost exclusively in the axils of taro, an aroid which was and is an important article of food ; even to this day, the roots, with the leaf bases on them, are frequently carried on sea voyages by Samoans, and they are transported raw to prevent decomposition : and as the egg of the insect is resistant to drying, everything favours distribution by human agency. This form has also been recently sent from Roviana, Solomon Islands, by Dr. E. G. Sayers. At Roviana the mosquito was captured on the verandah of a mission hospital. The mission at that place was established 40 years before, and a considerable number of Tongan teachers had been employed there, particularly in the early days. It is easy to think that the Tongan mission teachers brought taro plants and eggs of *A. kochi* var. *samoana* to Roviana.

If one studies the distribution of many of the insects which were probably transported by early man, curious anomalies appear. For instance, neither of

the Fulgoroids associated with taro and sugar (*Megamelus proserpina* and *Perkinsiella vitiensis*, p. 57 above) has reached the Hawaiian Islands; had they done so, they could not have escaped the economic entomologists of those islands, and in particular the late Mr. F. Muir, the authority on this group of insects. Rather similarly *Aëdes kochi samoana*, which breeds in water in the axils of taro, seems to be absent from the Society Islands and the Marquesas, in both of which it has been looked for: its absence from atolls (Ellice, Tokelau, etc.) is not surprising, for the taro which grows in their miserable soil is a different type, which does not hold water in its axils.

(2) Introduced Insects of Uncertain Status.—I have defined a group of insects which were probably introduced by the early Polynesians; they are obviously associated with the native life, and many of them show curious anomalies in their distribution. There remains a large group of insects, which may be truly native or may have been introduced either by Samoans or by Europeans. The difficulty of deciding may be illustrated by the cockroaches. Apart from the endemic species there are several cosmopolites (*Blattella germanica*, *Periplaneta australasiae*, *P. brunnea*, *Pycnoscelus surinamensis*); it is easy to attribute their presence to European ships. But how are we to treat *Eoblatta notulata*, *Cutilia soror* and *C. nitida?* These species have a wide distribution in the Malay Islands, and extend thence into the tropical Pacific: they may have reached Samoa by natural means, or with the Polynesians, themselves native of S.E. Asia.

The same difficulty is frequently encountered in other groups, for instance, the earwigs and the many Coccids; it is also impossible to feel any certainty about the means of arrival of the two species of scorpions, both of them widely distributed in the South Pacific. There are several small moths, such as *Setomorpha rutella*, which we bred from chicken dung and also from bread-fruit which had rotted and then dried, and which are known to breed in many sorts of dry refuse; such a species may be native, or may have reached Samoa by artificial means at any period. In the same ambiguous group one must place *Pyralis pictalis* and *manihotalis*, both bred from refuse in fowl-houses. One encounters the same difficulty among the Drosophilidae: several (*Drosophila ampelophila* and *errans*, *Spinulophila nasuta*) have a very wide tropical distribution in both hemispheres. One is inclined to attribute it to European shipping till one notices that other members of the family (*Mycodrosophila gratiosa*, *Hirtodrosophila seminigra*) seem to be native, occurring in Malaya and in the

Samoan hills : but if these arrived by natural means, why not the other, tropicopolitan, species ?

The dung-breeding insects are also of doubtful status. At first sight it seems likely that they arrived in ships, particularly if live cattle or other domestic animals were carried, and many of them are probably of recent European introduction. But others may have accompanied Polynesian travellers, and others again may be truly native : one must remember that dung of one sort or another must always have been available in Samoa. However they came, the dung-breeders are numerous and represent many groups of insects, e.g. several Sphaeroceridae ; *Milichiella luteipennis ;* that glorious Syrphid, *Volucella obesa ;* many Muscidae, etc. (*Musca*, *Stomoxys*, *Sarcophaga*, *Chrysomyia*) ; also the small chafer *Aphodius*.

(3) European Introductions.—The presence of many sorts of insects in Samoa is almost certainly due to European commerce. This is particularly clear if the species attacks some commodity which was not used by Polynesians in the old days. As instances one might quote the beetles eating dried foods : *Tribolium castaneum*, *Araecerus fasciculatus*, *Carpophilus hemipterus*, *C. dimidiatus*, *Tenebroides mauritianicus ;* also such moths as *Corcyra cephalonica*, *Ephestia cautella ;* the wood-eating beetles, *Lyctus brunneus* and *Minthea rugicollis ;* also beetles which are predatory on some of the above, e.g. three species of Cleridae. It also seems probable that insects which attack fabrics, feathers and skins have been recently brought in : such are *Dermestes vulpinus* and *Tinea pachyspila*. Another group are the parasitic insects, mostly introduced with European domestic animals or foreign rodents : *Xenopsylla cheopis*, from foreign species of *Rattus* and from *R.* (*Mus*) *exulans*, the native rat, an animal which was carried in canoes and which appears to have no fleas of its own in Samoa ; the human flea, *Pulex irritans*, apparently not present till the days of European shipping ; a sucking louse, *Polyplax spinulosa*, from ships' rats ; the tropical bedbug, *Cimex hemipterus* (ii, 160 ; also Buxton and Hopkins, 1927, p. 54). The Lygaeid, *Clerada apicicornis*, which has a wide tropical distribution and is found associated with rats' nests, may fall in the same group ; but it is equally likely that it toured the Pacific in canoes with *Rattus exulans*.

The hive-bee, *Apis mellifica*, is now common in Samoa, Tonga and other groups. As I can find no reference to bee-keeping among the Polynesians in the old days, I assume it to be a recent introduction.

There are also many agricultural pests, clearly of recent introduction. Of

these the most interesting is *Oryctes rhinoceros*, because the story of its spread is so fully told by Jepson (1912), Friederichs (1913) and Friederichs and Demandt (1922). It seems that larvae were introduced to Samoa, from Ceylon, in boxes of soil in which rubber trees were growing ; the introduction occurred at Apia in November, 1910. Extension of the insect's range was very rapid, and within little more than a year it had occupied the coast of Upolu westwards, for about 60 miles ; eastwards, that is to say in the direction from which the Trade Wind blows, it had only spread about 8 miles in the same period. The beetle became an extremely serious pest of the coconut, the source of the agricultural wealth of native and European alike, and so it still is, though partial control was achieved by hand-collecting. The system has already broken down more than once, at times of epidemic disease or political unrest. The introduction of Scoliidae, with a view to natural control, has been discussed many times since 1912, but I believe that nothing has actually been done.

Many of the other pests of crops are certainly of recent introduction. It seems unnecessary to name them here, for Hopkins (1927) has dealt with many of these insects and given a full list of earlier papers.

I cannot leave the subject of introduced pests without calling attention to the grave danger that many other insects will reach the Samoan Islands. When we lived in Samoa, in 1924 and 1925, every incoming boat used to bring fresh fruit, some of it grown in New Zealand, but most of it from New South Wales. Most of the fruit could well have been grown locally, and the trade was small and only met the needs of the more luxurious Europeans. But though I pointed out the danger, the Administration was too timorous to stop this importation, and I felt little doubt that the island would be colonized by the Mediterranean fruit fly (*Ceratitis capitata*) and other Trypetidae. Several troublesome species of *Dacus* have already been introduced. One should also mention the danger of bringing in timber-pests ; at the time when we were in Samoa, it seemed that there were no foreign termites, and that the indigenous species were well-nigh harmless ; there were also no tropicopolitan Cerambycids among the 35 species in the collections. Another insect which menaces the islands is *Anopheles punctulatus*. This species, which is a well-known carrier of malaria, occurs in Melanesia, as far east as 170° E. ; it is absent from Fiji and all Polynesia (Buxton and Hopkins, 1927, p. 67). There is a risk, though it is not great, that it may be introduced into Samoa, where its presence would presumably cause a great epidemic of malaria. In the event of its reaching Apia, it would find that everything possible

had been done to ensure its establishment, for the streams which run through the town have been dammed to make swamps for taro. It may be expected that many other troublesome insects will eventually arrive. *Piophila casei* is not yet known to occur, though it is recorded from Fiji by Bezzi (1928). The two species of *Dysdercus* which are recorded are only known to occur in Fiji and Samoa; in spite of the fact that some cotton and kapok is grown none of the more widely distributed and harmful species has yet been found in Samoa.

At the time when we were in Samoa it was useless to point out these dangers, for every one said that if the pests could have come they would have done so long ago; also that if they are coming, nothing would stop them; also that no one really knew anything till he had lived 30 years in the islands (the converse being more nearly true). I feel confident that the Samoan Islands will eventually possess all the cosmopolite pests which may to-day be seen in Oahu or in New Caledonia.

The insects mentioned above have come in with European trade or agriculture, but the white man has brought in many others quite casually. Among them are all the Samoan Vespids (*Polistes macaënsis*, and two species of *Odynerus*); also perhaps the bee, *Lithurgus scabrosus*. The two bees of the genus *Megachile* are more probably native, though members of this genus are so well known on ships; for both the Samoan species have developed endemic races, in some of the Samoan Islands and also in other parts of the Pacific. The predatory ants, *Pheidole megacephala* and *P. oceanica*, are also casual introductions, as are the mosquitoes *Culex fatigans* and *Aëdes argenteus*, the history of which in Oceania is described elsewhere (Buxton and Hopkins, 1927, pp. 83–85, 113–115). The dung breeders, many of which are probably recent immigrants, have already been considered. Berland (viii, 35) mentioned two widely distributed species of spider which were not recorded from Samoa by two earlier writers, but which occurred in our material. These, as he says, are doubtless very recent introductions, and he mentions another species which may yet be expected to follow them.

(4) Foreign Predators.—The general impression that the visitor carries away is that, in the hills, the native flora and fauna of Upolu and the other Samoan Islands is flourishing and in little danger of extermination. But round the coast, and particularly in the neighbourhood of Apia, which has always been the main harbour, the situation is different. For one thing, the Samoans live, and always have lived, along the beach, where they have their villages and most

of their plantations. The Europeans and half-castes live in the same zone, principally round Apia. Here, therefore, settlement has dispossessed the native flora, and the insects dependent on it. But it seemed that introduced insects were also playing a part, for even when one could find patches of forest near the coast, as in Luutuanuu, Aleipata and elsewhere, the insects were few and uninteresting. This may be due to the introduced wasp, *Polistes macäensis*, and to various ants, of which perhaps the most important are *Pheidole oceanica* and *P. megacephala;* both these insects were collected as high as 2,000 feet at Malololelei, on Upolu. It will be remembered that Perkins (1913) found the latter species to be the most abundant of foreign ants in Hawaiia, and blamed it for the disappearance of much of the native fauna; he said, "save for a few forms that can resist, or are tolerated by the ants, the endemic fauna is entirely exterminated. This native fauna, especially the beetles, appears as if by magic, the moment the limit of range of *Pheidole* is reached." In Samoa we did not form the impression that the case was so desperate, but it is impossible to be certain. There seems to be only one insect about whose disappearance definite information exists: the Geometrid moth, *Cleora samoana*, the extreme variability of which makes it one of the most interesting insects in the country (iii, 158 and Plate V) was collected by Rechinger in 1905 at Malifa and Motootua, which are just outside the town of Apia, within a couple of hundred feet of sea-level (Rebel, 1910). Hopkins and I lived and worked for two years in the same neighbourhood, in which we never observed this moth. The lowest point at which we obtained it, in 1924 and 1925, was Vailima, 600 feet above sea-level. Here and also at Malololelei, 2,000 feet, it was common; it is to be hoped that it may remain so, or at least that we may from time to time learn more of its status.

In the systematic part of this work, particular attention is given to precise localities and dates of capture, because these may eventually give information about the status and fate of the native fauna.

Taxonomic Notes

The Endemic Insects.—The naturalist who works on an island remote from large areas of land has at least one question always in his mind: is the fauna around him continental or oceanic? He may obtain a partial answer to this question by remembering that there are two characters of insular faunas: they show a high proportion of endemic species and frequently of endemic genera;

they are also remarkable for the absence of larger or smaller groups widely distributed in the world and found in neighbouring continents.

(1) The Proportion of Endemic Species.—It appears from Table I that 1,603 species are known to occur, of which 787 (= 49%) are endemic. It is clear that the proportion of endemic species is high in the insects of all orders : this suggests that the Samoan fauna is oceanic, a conclusion already reached after considering the flora, and the fauna in general (ix, 24).

It must be realized that when our knowledge of the insects of the south Pacific is more complete, a number of species now thought to be endemic in Samoa will be found to occur in Fiji, Tonga or elsewhere. On the other hand, further collecting in Samoa will certainly increase the list of the endemic fauna, many of the members of which are small and difficult to obtain. We may perhaps conclude that the proportion of endemic forms will not be greatly altered as knowledge increases. This has actually occurred in the Hawaiian Islands. Perkins (1913) gave a list of 3,325 species known to occur, of which 82% were thought to be endemic. With the passage of years the total number has been raised a full third, to 4,620, but the endemic proportion is 81% (Bryan, 1934).

The proportion of endemic species in the whole insect fauna of other tropical archipelagos is not known, except for Seychelles : according to Scott (1933), 2,090 species of insect are known of which 65% (1,366) are endemic. It would, of course, be possible to gather together a large body of fact about the proportion of endemics in particular orders or families in insular faunas ; for instance, of the 239 Brachycera and Athericera of Fiji, 60·5% (144) were endemic (Bezzi, 1928). But I have not put myself to the trouble of obtaining such figures.

But the proportion of endemic species among the insects as a whole, or even in particular orders, is a crude figure, for the different families, etc., can hardly be compared with one another. For instance, we find (Table 1) that 58% of the Diptera are endemic, and among the 100 Nematocera (vi, 24) the proportion is almost identical (60%) But if individual families are considered, one finds that only 1 out of 7 Culicidae is endemic, whereas 23 out of 33 Tipulidae (70%) and 10 of the 16 Ceratopogonidae (60%) are unknown from other parts of the world. The same holds good of the Neuroptera (vii, 89). Of the 5 Samoan species of Hemerobiidae, 4 are endemic and belong to endemic genera. In contrast there are 9 Chrysopidae, of which 1 is the sole representative of an endemic genus. The 8 others are referred to the widely distributed genus *Chrysopa ;* 2 of the 8 seem to be endemic, and 2 others seem to be peculiar to

TABLE 1.

Showing Orders of Insects recorded from Samoa; the Number of Samoan Species in each; and the Number of Species which at present appear to be endemic.

ORDER	TOTAL SPECIES	ENDEMIC SPECIES	ENDEMICS *Per cent.*
Thysanura	4	2	—
Collembola	4	1	—
Orthoptera	77	35	45
Dermaptera	12	5	—
Isoptera	7*	6*	—
Psocoptera	11	7	—
Anoplura (with Mallophaga)	14	1	—
Ephemeroptera	1	1	—
Odonata	28	12	43
Thysanoptera	3	3	—
Hemiptera	247	127	51
Neuroptera	15	7	—
Trichoptera	1*	1*	—
Lepidoptera	442	191	43
Coleoptera	385	202	52
Hymenoptera (not Parasitic)	57	15	26
Diptera	292	171	58
Aphaniptera	3	0	—
Total	1,603	787	49

* One undescribed.

the Central Pacific: the other 4 have a wide distribution, and several occur in Australia. Among the Myrmeleonidae, very few occur in Polynesia, but 2 of them have a very wide distribution. The fact that species of *Chrysopa* and *Eidoleon* range so widely, and that they appear to be able to cross great stretches of ocean is unexplained; indeed, I do not think that attention has previously been called to it. Another group of creatures in which endemicity is high, but not equally so in all families, is the Araneida, already discussed (p. 45 under "wind").

In certain groups of insects, and particularly in those which possess great powers of flight, the proportion of endemic species is low. This is well seen in the Odonata. Ten of the 15 large and powerful Anisoptera have a wide distribution outside Samoa, and several of them are known to occur on other remote

islands : but among the more delicate Zygoptera, 10 of the 13 species are peculiar to Samoa. Moreover, in several families of Diptera Brachycera and Athericera, especially those which contain robust species of powerful flight, the proportion of endemic species is low. This is illustrated by the following numbers :—

	Total.	Apparently endemic.	Known from elsewhere.
Stratiomyidae	7	3	4
Tabanidae	1	1	0
Asilidae	4	2	2
Syrphidae	10	1	9
Total	22	7	15

(2) Production of Endemic Complexes.—Among the insects found in oceanic islands, two related phenomena have occasionally been noticed. There may be very great variability within the limits of a single species on one island : there is also a tendency for the production of groups of closely related species, some or most of them peculiar to single islands within an archipelago.

We have seen that the proportion of endemic species is high among the Samoan insects, and it would be interesting to find out whether either of these other phenomena is observable. It seems certain that examples of great variability are few, with the exception of that wonderful Geometrid, *Cleora samoana ;* this insect exhibits an extreme degree of variation in colour, pattern and size ; moreover, teratological varieties appear to be unusually common (Prout, iii, 158). Though much attention was devoted to the variation of this species, it was not found that it was associated with season or with place : indeed, all the insects figured on Plate V, Part iii, were taken on one night in one house. It also appears that little if any of the variation is due to sexual dimorphism. Two other examples of variability are commented upon in the text : the Lycid, *Samoaneros acuticollis*, and the Chrysomelids of the genus *Stygnobia*. Maulik (iv, 191), after studying a long series of *Stygnobia*, calls attention to the fact that in an insular fauna a species may be more plastic than in a continental area. The phenomenon has been observed in several groups of Hawaiian insects and is mentioned in the summary of the Fauna Hawaiiensis (Perkins, 1913). It is possible that in the rather simple fauna of an island some type of competition is

less than it would be in a continental area, permitting species to develop a high degree of variability. In Hawaiia, but not apparently in Samoa, variability is associated with the formation of groups of closely related species.

As to the other characteristic of island faunas—the production of large groups of closely related, endemic, species—the Samoan fauna provides few examples. For instance, among the Microlepidoptera (in which two-thirds of the total species are endemic), the 90 endemic species are distributed among 54 genera, so that the number of species per genus is low : moreover, the 8 endemic genera are all monotypic, and they belong to 6 families. There are, however, 2 genera which show some development of endemic species ; 15 of the 17 *Labdia*, and 7 of the 9 *Decadarchis*, are endemic. The figures for the Nematocera are not dissimilar : the number of species per genus is under 2 : there are only 2 * endemic genera, each of them monotypic. It should, however, be mentioned that there are 9 species of *Trentepohlia* (Tipulidae), 8 of them endemic. Similar figures could be given for other groups of which we have adequate knowledge. In the Curculionidae the 86 species are distributed among 55 genera. One genus, *Trigonopterus*, has 9 species, another, *Cossonus*, has 4 ; all the species in both genera are endemic.

There are two or three groups of endemic species which are sufficiently striking to call for mention, though the number of species is not very great in any of them. The smaller dragon-flies were carefully collected at least in a part of Upolu ; among the Coenagrionidae there is an interesting development in *Ischnura* and related genera (*Amorphostigma*, *Pacificagrion*). *Ischnura* contains 5 Samoan species, 1 (*I. aurora*) which is known to be distributed by wind (p. 44) and ranging widely, and four which are endemic. *Amorphostigma* contains 2 species, both endemic, and *Pacificagrion* 1, also endemic. The interest of the group is increased, for Fraser says that certain archaic features are discoverable in them. The rather similar development of the Agrionid *Nesobasis* in Fiji should be remarked (Tillyard, 1923). The Samoan Halictine bees are interesting in a rather similar way. As at present classified, there are 4 closely related endemic species in *Halictus*, and 2 in the endemic genus *Echthralictus*. These particularly interesting insects are discussed elsewhere by Perkins and Cheesman. Here it seems sufficient to call attention to the need for collecting them in Fiji and

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* When Edwards' account of the group was written there were 3 endemic genera. One, *Pontomyia*, has since been found in Japan (Tokunaga, 1932).

Polynesia, and to the very interesting biological question which is suggested by the structural characters of *Echthralictus*. Another small group of endemic species is found in *Mordellistena* (Mordellidae): in Samoa there are 2 species which range widely in Fiji or Melanesia, and 5 endemics, each of them already known from Upolu and Tutuila.

It seems then that complexes of closely related endemic species have not developed in Samoa. But the Samoan fauna contains representatives of groups which have developed endemically in central Polynesia and are characteristic of that area. One might quote the Cicadellid genus *Jassoidula*, described in the present work as new, to which Osborn attributes 8 species: 4 are endemic to Samoa (1 Upolu; 1 Upolu and Savaii; 2 Tutuila), 3 are endemic to Tonga (1 each on Vavau, Haapai and Nukualofa), and 1 to Niue. Numerous other examples can be found in the pages of this fauna; for instance, the Lycid genera *Melaneros* and *Samoaneros;* also the Hydrocampinae, *Piletocera* and *Bradina.*

(3) Peculiar and Anomalous Genera.—An island fauna might demonstrate its antiquity by preserving very ancient types, or by developing endemic and highly peculiar forms of life. We may say at once that there are no living fossils among the Samoan insects, or indeed among the other animals or the plants. But several peculiar endemic genera have been discovered in the collections. Much the most remarkable is the submarine Chironomid fly *Pontomyia.* The anatomical characters of this insect were fully described and figured by Edwards (1926b); briefly, the male has greatly reduced paddle-like wings, with what appears to be a hinge across the middle of them; it shows several other peculiarities, any one of which would render it almost unique in its family. The female is cylindrical and entirely without mouthparts, antennae, front legs or wings; the middle and posterior legs are greatly reduced; the insect is as much simplified as any known Dipteron. We were so lucky as to collect a large number of adults, and also what appear to be the corresponding larvae and pupae. The early stages were found among beds of *Halophila*, a flowering plant (Hydrocharitaceae) which grew in sandy patches in the shallow sea inside the coral reef. The adults were obtained by tow nets, after dark, and appeared to exhibit lunar periodicity. Such biological observations as I could make, and a discussion of the failure of the Insecta to colonize the sea, have been published elsewhere (Buxton, 1926). Since that date a very similar member of the genus, till then supposed to be entirely peculiar to Samoa, has been discovered by Tokunaga

(1932) in Japan. This author has been able to add greatly to what is known of the structure and habits of *Pontomyia*. He confirms my observation of the existence of lunar periodicity, and says that copulation occurs on the surface of the water, the female laying all her eggs at once and dying within an hour of emergence. On several points Tokunaga's observations cannot be reconciled with my own, which is remarkable, for the anatomical specialization of both species is so extreme that one would expect them to live nearly identical lives. Among other matters Tonkunaga says that the male of the Japanese species uses its wings only for gliding on water, and he adduces evidence which appears to show that its unique structure fits it for this purpose and no other ; whereas I was never able to see the Samoan species use its wings, though I observed that the long first and third legs were used for propelling the insect beneath the water. Moreover, the Samoan species was caught alive, in tow nets, and it was frequently found in the lagoon when the tidal current was so strong that one could not swim against it ; it was associated with patches of *Halophila*, in which the female pupae were discovered. Whereas the Japanese species appears to have no association with the plant, and to live in pools between tide-marks. It seems, therefore, that in spite of similarity in structure, there are considerable differences in biology between *Pontomyia natans* in Samoa and *P. pacifica* in Japan, and that the former is the more oceanic or planktonic in its habits. It is perhaps a little disappointing that *Pontomyia*, which appeared to be the peculiar glory of Samoa, should be re-discovered in Japan : it is presumably a widely spread insect, which has escaped detection because of its peculiar habits.

The present work contains descriptions of several other insects which are remarkable in structure or puzzling in their systematic position. For instance, the Fulgoroid genus *Buxtoniella*, described by Muir (ii, 23) to contain 2 endemic species, was placed in the Lophopidae ; but its position was an enigma, the external characters suggesting an Issid, the genitalia of both sexes showing Lophopid characters. Subsequently, the same author (Muir, 1931, pp. 78, 79) described the genus *Painella*, containing 2 species from the Solomons : this genus resembles *Buxtoniella*, but the affinities remain obscure. Several other Hemiptera of obscure affinities have been discovered in Samoa ; for instance, the Lygaeid *Bryanella*, which appears to be intermediate between the Myodochini and the Rhyparochromini ; and *Moana*, a Cicadid of which the venation is extremely aberrant.

One might quote other genera, the systematic position of which is obscure,

But none of the specialists who have contributed to our knowledge of the fauna has found it necessary to erect a new tribe or subfamily for the reception of a Samoan insect: they describe many endemic species and genera, but nothing of higher taxonomic rank.

(4) Species confined to Parts of the Samoan Archipelago.—It is tempting to endeavour to assess the age of the Samoan fauna by discovering how many of the endemic species are widely spread within the archipelago, and how many are peculiar to one or two islands. But at present this is difficult, for only in a few instances do we possess enough evidence. It has to be remembered that most of the collecting on different islands was done by different men, and the apparent absence of an insect may often be due to this personal element. One observes, for instance, that the Nematocera and Microlepidoptera were thoroughly worked by Mr. Hopkins and myself on Upolu, very little on other islands. Generally speaking, one can attach most importance to absence from Upolu, for its insects were collected by many men, and at all times of year.

But there is at least one group of insects, the butterflies, on which we may feel that conclusions are solidly based. This is partly because good material is available from all the larger Samoan Islands and from other archipelagos, and partly because the principal collector of them, Mr. Hopkins, is also the author of the systematic paper. From his work (Table 2), it appears that 3 of the 28

Table 2.

Showing Distribution of Races of three Species of Butterfly, within the Samoan Archipelago. The + sign signifies that the race is present, the 0 that it is very definitely absent.

	Upolu.	Savaii.	Tutuila.	Manua.
Danaida melissa melittula .	++	++	0	0
,, ,, *tutuilae* .	0	0	++	?
Hypolimnas bolina inconstans .	++	++	0	0
,, ,, *pallescens* .	0	0	++	+
Precis villida samoensis . .	++	++	0	0
,, ,, *villida* . .	0	0	++	+

species of butterflies which occur in Samoa have produced races endemic to certain islands. In each case the race in Upolu and Savaii (Western Samoa) is

the same, and differs from that in Tutuila * ; the Tutuilan race is already known to occur in Manua in two of the three species. *Danaida melissa* has produced two endemic races in Western Samoa and Tutuila : *Hypolimnas bolina* and *Precis villida* have developed endemic races in Western Samoa, but the forms in American Samoa are found in Tonga and elsewhere. We must return to the Samoan butterflies when we discuss the geographical relations of the insect fauna. For the moment it suffices to remark on these three species, which have developed island endemicity.

In the Heterocera there are one or two endemic species which occur only in a part of the Samoan Archipelago. The conspicuous Lithosiid, *Chrysaeglia samoensis*, is common on Upolu, and has been collected on Savaii ; but it has never been taken on Tutuila, and it seems highly probable that it does not occur in American Samoa. It appears almost certain † that the two species of *Deilemera* (Arctiidae) have a similar distribution. *D. alba* is a white day-flying moth, abundant and very familiar on Upolu and Savaii. In the course of one's first walk on Tutuila, one remarks the absence of the white insect, and the abundance of the black and white *D. mundipicta samoensis*, which also occurs in the Manua group, but is unknown in Western Samoa. In the field the difference is extremely striking.

In order to show that species endemic to single islands have not frequently developed, Table 3 has been prepared : I have taken some trouble to collect these examples. At first sight the table appears to show much evidence of island endemicity, but the reader will see that many insects which appear to be confined to one island have been collected on a single occasion only. With increased knowledge the proportion of island endemics would probably become less. Among the insects shown in the table it seems that good evidence of island endemicity is only shown by *Stygnobia aenescens*, *Trigonopterus submetallicus*, *Megachile scutellata*, *Eucarobius* spp. The table might be extended to include the following and others :—*Anaxipha* (Gryllidae ; four species on Upolu, Savaii and Tutuila, five species from a single island : it should be observed that the

* Upolu and Savaii, with Apolima and other small islets, lie within one 100-fathom line. But east of Upolu the bottom falls to very great depths, nearly all the interval between Upolu and Tutuila being deeper than 1,000 fathoms. There is a similar deep channel between Tutuila and Manua. Contrast Fiji, almost the whole of which is within one 1,000 fathom contour ; Tonga is substantially similar.

† There is a single record (iii, 193) of *D. alba* from Ofu, Manua group. I am personally convinced that this must be due to erroneous labelling, either in the field or the museum.

TABLE 3.

Showing the Distribution within Samoa of certain Groups of Species which exhibit island Endemicity. The Distribution is given under the separate Islands, ++ indicating that a Species was collected on many Occasions, + on several Occasions, and 1 once only.

	UPOLU.	SAVAII.	TUTUILA.	MANUA.
CHRYSOMELIDAE				
Stygnobia aenescens			++	
,, *cauta*	++	1	+	1
,, *variabilis*	++	++	++	
,, *minuta*	+		+	
CURCULIONIDAE				
Sphaerorrhinus puncticollis *			+	1
Acicnemis eludens †	1		+	
Trigonopterus crinipes	++	+		
,, *submetallicus*			+	
,, ,, *mendax*	++	1		
,, *caesipes*	1			
,, *aeneoniveus*	++	1		
,, *bicolor*			+	
,, *serratipes*		1		
,, *bryani*			1	
,, *samoanus*	1			
,, *binotatus*			1	
Cossonus platyrrhinus	1			
,, *dentipes*	+		1	
,, *limbaticollis*			1	
,, *quaerens*	1	1		
,, ,, *afonus*			1	
MEGACHILIDAE				
Megachile diligens armstrongi	+			
,, ,, *calens* ‡			1	
,, ,, *buxtoni* ‡				
,, *scutellata wilmattae*	++			
,, ,, *tutuilae*		+		
HEMEROBIIDAE				
Eucarobius fasciatus			++	
,, *graeffei*	1	1		
,, *oblongus*	++	+		

* The three specimens from Manua differ from all those from Tutuila in colour of scales.

† The single specimen from Upolu differs conspicuously from the three from Tutuila; but on this material one cannot say whether the variation is random or insular.

‡ The distribution of these forms leaves much to the explorer of the future. The record of *calens* from Tutuila rests on a single specimen, and though it seems absent from other Samoan islands it is recorded from Fiji and Ellice Islands. *Buxtoni* is described from a single male from Manono, but is probably not confined to this small island which lies within the main coral reef surrounding Upolu.

Gryllidae of American Samoa are most imperfectly known): certain Drosophilidae (endemic genera, *Samoaia* and *Upolumyia*, and endemic species in *Drosophila* and other genera): *Prosoplus* (Cerambycidae; one species frequent on Upolu, another on five occasions on Tutuila): certain other Cerambycidae (see table of distribution, iv, 135).

In contrast with these there are several genera which contain a considerable number of Samoan species, not one of which is confined to a single island: for instance, *Mordellistena* (Mordellidae), contains 7 Samoan species, 2 of which are known from other archipelagos: every one of the 7 occurs both in Western and American Samoa.

It is necessary to be extremely cautious in accepting evidence that species are confined to particular islands in Samoa. There are several insects which appear to be locally distributed, though they probably exist in all parts of the archipelago. One might mention two Lygaeidae: *Nysius pacificus* was collected on Tutuila by three collectors on at least five dates, but never found in Upolu or Savaii, though it is known from Efate, New Hebrides: *Orthaea limbata* was collected on Savaii on ten different dates, and once on Tutuila, but there is no record from Upolu: this is the more remarkable as this bug is recorded from Fiji and Niue. It is impossible to believe that these insects, so widely spread in the Pacific, are absent from Upolu.

One might summarize this section by stating that only a few insects have developed separate races or species in different parts of Samoa. But when this has occurred, one race or species occurs in Upolu and Savaii, and another in Tutuila (and frequently Manua). In the slight development of island endemicity Samoa appears to resemble the Seychelles (Scott, 1933). In Hawaiia, on the other hand (Perkins, 1913), and also in the Marquesas (Mumford and Adamson, 1934), many genera have produced a wealth of species confined to single islands.

The Absence of Certain Groups.—It is a general characteristic of an insular fauna that certain groups of organisms are absent, though they occur on the continents in the same part of the world; other groups, which are represented on the island, comprise a disproportionate part of the fauna. The Samoan material seems to be adequate, and it is possible to examine the fauna and call attention to those groups which are absent, or which are present in disproportion. The subject is of interest because it may throw light on the origin of the land fauna of Polynesia.

(1) Absence and disproportionate Representation of Orders.—If we consider first the representation of the orders of insects, it will be observed (Table 1, p. 67) that 18 of them are represented in Samoa. Five orders * appear to be absent. With regard to 2 of these, the Protura and Strepsiptera, one must admit that they may be present and unrecorded, because the necessary specialized collecting was not undertaken. The other 3 orders, the Plecoptera, Embioptera and Mecoptera, are not represented in the material, in spite of the considerable collections of insects which were made in places where these insects would be expected to occur. The absence of the Nemourid stone-flies is remarkable, having regard to their wide distribution in the world and their existence in Australia, New Zealand and South America. It appears to me to be unlikely that representatives of these 3 orders occur in Samoa. A sixth order, the Siphonaptera, contains several species which are of recent introduction to Samoa, but only one which may be native.

Apart from the total absence of certain orders, the disproportionate representation of others is remarkable. Of the 18 orders which have been found in Samoa, 2, the Trichoptera and the Plectoptera, are there represented by a single species. With regard to the second, one notices that it seems to be the most easterly outlier of a genus (*Chloëon*) well represented in south-east Asia.

One may therefore say that out of 23 recognized orders of insects, 5 are absent from Samoa so far as we know ; a sixth is not represented by any species which is certainly native : 2 others are represented only by single, but endemic, species. The great bulk of the fauna is therefore contributed by 15 of the orders.

It is interesting to compare the representation of certain orders in Samoa with what is known of the Seychelles (Scott, 1933), Hawaiia (Perkins, 1913 ; Bryan, 1934) and the Marquesas (Mumford and Adamson, 1934), information about which is not yet completely available.

	Samoa.	Seychelles.	Hawaiia.	Marquesas.
Protura . . .	No record	Unknown when material collected	No record	No record
Strepsiptera . .	No record	One endemic	Two species, One endemic	No record
Plecoptera . .	Absent	Absent	Absent	Absent

* For the sake of uniformity we adopt the 23 orders given by Imms (1934).

	Samoa.	Seychelles.	Hawaiia.	Marquesas.
Embioptera . .	Absent	One	One, endemic	One
Mecoptera . .	Absent	Absent	Absent	Absent
Siphonaptera . .	Several, apparently introduced	One, introduced	Five, introduced, endemic	Three, introduced
Plectoptera . . (Ephemeroptera)	One, endemic	One, endemic	Absent	Absent
Trichoptera . .	One, endemic	Six, endemic	Absent	Absent

The general resemblance between the faunas of Samoa and these other archipelagos is remarkable: no simple geographical explanation seems to cover the facts.

(2) Disproportionate Representation among Families and Other Groups.—With regard to other groups of insects which are absent, a complete list for any order could be made by referring to the systematic Parts of this work, having due regard to the fact that the collections in certain orders are admitted to be very incomplete (p. 37). It is sufficient here to point out some of the more obvious and interesting absentees.

Of the Orthoptera, it seems that the Mantidae are absent, though there is an old record of *Tenodera* based on a specimen which was stated to have been collected on Upolu; Chopard disregards this and says that none of these insects occurs east of the Solomon Islands, though it seems that two genera (but not *Tenodera*) have been recorded from Fiji (Holdhaus, 1929, pp. 680–681). The Gryllacridae afford another interesting problem. According to Karny (1929), their distribution in the Malay Islands and Oceania is extremely interesting. It is therefore much to be regretted that the Samoan record is doubtful. The species, *Gryllacris oceanicus*, was collected by Le Guillou in 1841; neither Rechinger nor any subsequent collector obtained material, and since Le Guillou collected insects on many groups of islands, I am inclined to suggest that the Samoan record is due to an error in labelling. On the other hand, both Chopard and also Karny, to whom the matter has been referred, point out that these are insects of specialized habits and express the view that the species may eventually be rediscovered. Moreover, according to Karny, *oceanica* falls in the *dubia* group, which is represented in Fiji and the New Hebrides, so that its occurrence in Samoa would be in no sense anomalous. Another Orthopteran which is

absent from Samoa is *Gryllotalpa ;* it appears that representatives of this genus occur in Australia and New Zealand, also in the Malay Islands, including New Guinea, also in New Britain and New Caledonia ; but these insects are not known to occur in the Solomons, and New Hebrides, also Fiji and all parts of Polynesia (Chopard, letter).

Even among the Orthopterous families which are represented in Samoa there is considerable disproportion. The Phasmids are represented by two species of *Graeffea*, a genus which may owe its present distribution to native journeys, as it is associated with the coconut, and by a species of *Nisyrus*. Members of this latter genus have a wide distribution in Melanesia, and have been recorded from Fiji and Tonga ; as the female is wingless, it has been held that this distribution is evidence of former land connections (Holdhaus, 1929, pp. 653, 681). The Acridians are represented by only 7 species, the Blattidae by 22, of which about 6 seem to be native ; all or nearly all the others have been introduced by man, but not necessarily within recent years. In contrast with these families the Gryllidae number 34 species, most of them endemic, and many of them brachypterous or wingless : the Gryllidae make up 44% of all the Orthoptera, excluding the Dermaptera. Chopard expresses the view that it is the hygrophile Orthoptera which are best represented in the fauna of Samoa. It is perhaps for the same reason that the Gryllidae are relatively numerous in the Seychelles (Scott, 1933) and Hawaiia.

From the order Hemiptera there are certain very remarkable absentees. It appears that of the 33 species of Coccidae which have been collected, only three can be regarded as endemic. In this respect and in many others, the Samoan insects present a contrast with those of Australia and New Zealand. In those countries, and especially in Australia, native species are numerous, and contain representatives of all the subfamilies into which the Coccidae are divided (Tillyard, 1926). Moreoever, there are no native species of Aphididae of Aleyrodidae in Samoa. Among the Heteroptera, the Samoan fauna includes representatives of all the more widely spread families, though 31 of the recognized 48 families are not recorded from these islands (ii, 82). The absence of those powerful insects the Belostomatidae is remarkable, especially as *Lethocerus indicus* is distributed from India to Australia (Tillyard, 1926, p. 157).

It appears that few important families of Lepidoptera are unrepresented in Samoa. Indigenous Pterophoridae are absent, as they are from Fiji, and eastern Polynesia (Meyrick, 1928) ; Meyrick (ii, 67) calls attention to their

absence, which is remarkable because the adults appear to be constructed so that they can be carried by wind, and the larvae of some of the species are polyphagous. The absence of the Oecophoridae is still more curious. These small moths are numerous in the countries which surround the Pacific, but no representative of the family occurs in Samoa (though we collected 113 species of Tineina), or in Hawaiia. Only a single species is known to occur in Fiji (iii, 67): another is recorded from the Society Islands, but there are grounds for thinking that it may have been carried there by man (Meyrick, 1928). Among the Geometrid moths there is a curious example of disproportion. In most parts of the world the Geometrinae form 30% to 50% of this family, but in Samoa there are only 4 out of a total of 30 species. It appears that a similar disparity has been observed in Melanesia and Polynesia generally, with the exception of Hawaiia, where the ratio is disturbed by the great development of a single genus. There are several other interesting absentees among the Lepidoptera. Members of the genus *Scoparia* (Pyralidae) are well represented in the faunas of islands, in many parts of the world. Meyrick informs me that he has described a species from Papua, but it seems that none are known from Melanesia, Fiji or Samoa. This might possibly be attributed to imperfect collecting, were it not that we failed to find *Scoparia* in Samoa in spite of much successful collecting of small moths; indeed, there are no Scopariinae from Samoa, though 119 species of Pyralidae are recorded. It must not be overlooked that *Scoparia* has reached Hawaiia, where it has developed a wealth of endemic species. Members of the genus are also recorded from the Marquesas, Tahiti and Rapa (endemic species in each, Meyrick, 1929).

The curious distribution of the butterfly, *Libythea*, absent from Samoa and present on one island in the Marquesas, is discussed below.

It is unnecessary to refer in detail to the distribution of families, subfamilies and species of large Heterocera, for Tams tabulates their occurrence in Samoa, Fiji, Australia and New Guinea. But one family, the Zygaenidae, may be mentioned, because certain of its members which are pests of coconut have been intensively studied. Several are known from Java and the great Malay Islands, others from New Guinea, the Bismarcks and the Solomons; none has yet been found in the New Hebrides, Fiji or Polynesia (Tothill, Taylor and Paine, 1930).

A considerable number of families of Coleoptera, including some of wide distribution, are not known to occur in Samoa. This may be in part due to insufficient collecting; but though neither Hopkins nor I have an adequate know-

ledge of these insects, several of the collectors from the Bishop Museum made satisfactory collections of beetles. Let it suffice for the moment to call attention to the absence of the Cicindellidae. Of these insects an endemic species has been recorded from Fiji, and others exist in the Loyalty Islands and the New Hebrides, as my friend Dr. W. Horn tells me by letter: none are known from Samoa. Several authors have called attention to the disproportionate representation of some of the families. Among the Lamellicorns, the Lucanidae are well represented, but there is a dearth of Scarabaeidae; as the former breed in rotten wood and the latter in soil, it is suggested that the facts point to colonization by drifting logs rather than by land continuity (iv, 35). Among the weevils, of which a considerable collection was made, the subfamilies which frequent bark are well represented; of those which eat leaves, very few species were collected, in spite of the fact that we devoted much time to beating the branches of trees and shrubs.

The paucity of Hymenoptera * in Samoa strikes one at once, and a reference to Part v of this work will show what a large number of families are not represented. It seems that there are no Chrysididae, in spite of the occurrence of insects which they might parasitize. The entire absence of saw-flies (Chalastrogastra) of all families is remarkable. According to Kuznetsov-Ugamsky (1926), the area which includes Australia, New Guinea and some of the adjacent islands is inhabited by a small but interesting fauna of saw-flies, some of which belong to endemic subfamilies. The eastern limit to which these insects extend does not appear to be defined, but it seems that Samoa is outside it. Saw-flies are also unknown on the Marquesas (Mumford and Adamson, 1934).

Among the Diptera Nematocera, the absence of the Bibionidae, Simuliidae and Blepharoceridae is remarkable, especially as extensive collections were made of other Nematocerous families. Dr. F. W. Edwards tells me by letter that he knows of no Bibionids in Fiji, but that *Bibio* and *Plecia* are represented in the New Hebrides. He calls attention (vi, 26) to the fact that a high proportion of Samoan Nematocera breed in decaying organic matter: he finds evidence of this in several families. He remarks also on the absence of larger and more robust Nematocera, not only Bibionids, but also Tipulini. Of other crane-flies (Tipulidae) a large collection was made, so that the absence of the large Tipulini is significant; I understand that they are numerous in the Oriental region, reaching their eastward limit in Fiji (*Ctenacroscelis*, three species). A Blepharocerid,

* The parasitic families have been excluded from this work.

Apistomyia, is known from Queensland, but there are apparently no records of any member of this family from New Guinea or Melanesia. The apparent absence of Simuliidae is remarkable, in view of the care with which we collected in one or two ravines and of the fact that several members of this family occur in Tahiti and the Marquesas : the matter is discussed on p. 87.

Among the higher flies, it will be noticed that the Anthomyinae are absent from Samoa, and also from Fiji ; it is understood that these flies are not numerous in the Indo-Malayan and Australasian areas.

The Odonata of Samoa are interesting, and they were carefully collected, particularly by Armstrong. Fifteen species of Anisoptera are known, belonging to the Libellulidae and Aeschnidae ; the Gomphidae and Cordulegastridae appear to be absent. Among the Zygoptera all the 13 species belong to the Coenagrionidae, 8 of them being referred to *Ischnura* and closely related genera ; there are no Agrionidae.

Esben-Petersen points out that the Neuropterous families Ascalaphidae, Osmylidae and Mantispidae are absent from Samoa and from all parts of Polynesia, in spite of their wide range in the world. Only one Myrmeleonid is recorded ; another species, *Eidoleon* (*Distoleon*) *bistrigatus*, was originally described from Tahiti, and is known to occur also in Raiatea and the Tuamotus, also in Hawaiia, Fiji and Australia. Its absence from Samoa is remarkable (vii, 91 : also Cheesman, 1927).

Our list of Apterygota includes no member of the Japygidae, but an endemic species has been collected and recently described by Silvestri (1930).

The Samoan spiders are rather well known, and show absence of certain families and great development of others. The possible relation of this to dispersal by air is discussed elsewhere (p. 45).

Two general conclusions emerge from the consideration of insects which are absent from Samoa. Many widely distributed families of several orders are not represented, as is typical in an oceanic fauna. In almost every case the family or order exists in the lands to the west and is not found farther east in Polynesia. Some of the groups which are absent in Samoa have extended eastwards to Fiji but no farther : others reach their limit in the New Hebrides and the Solomon Islands : others again have not extended even into Melanesia. One may say, therefore, that a study of the absentees shows clearly, as does a study of the forms known to exist in Samoa (p. 83), that the fauna has reached these islands from the west.

III. THE INSECT FAUNA: ITS ZOOGEOGRAPHICAL RELATIONS

High and Low Islands Contrasted

Before we study the zoogeographical evidence which is provided by the Samoan insects, it is well to recall several facts of a general nature which could not be ascertained from a study of maps alone. The naturalist in the Pacific learns at once that he must distinguish high from low islands. The high islands are volcanic and very fertile: they are covered with a dense flora and fauna. The low islands or atolls are very small; they barely rise above the level of the sea, so that the subsoil water is generally brackish. In these places the whole flora belongs to the strand association, and the island only contains a very few species of plants and animals, all or nearly all of them of the widest possible distribution.

It seems that Holdhaus (1929, 1934) hardly gave sufficient attention to this distinction between high and low islands when he defined the subregions of his Australian Region. His Melanesian subregion stretches eastwards to include Fiji, Samoa and Tonga, high islands being characteristic of these three archipelagos. His Polynesian subregion includes a rather heterogeneous collection of other islands, and stretches from Jaluit and the Gilbert and Marshall Islands through Tahiti and Eastern Polynesia to Easter Island. Many of the islands in this group are atolls, for which reason their fauna and flora is very poor. The contrast between the richness of Holdhaus' Melanesian and the poverty of the Polynesian subregion is rather due to the type of island than to zoogeographical causes, and one doubts whether the division into subregions is justifiable. A rather similar case has been discussed by Scott (1933); in the area which he considered, the Seychelles Islands were high and fertile with a large endemic flora and fauna; the other islands—Aldabra, the Chagos Islands, etc.—consist of coral a little elevated above sea-level and carrying a poor flora and fauna and few endemic species. But Scott, perhaps because he was personally familiar with the area, realized the essential unity of his islands, in spite of their superficial differences.

But even in those Pacific archipelagos which contain high islands, considerable geological differences exist. If we are discussing the insects which inhabit Fiji, Samoa and Tonga, we should not forget that the archipelago of Fiji contains

much the largest islands with some ancient rocks. This archipelago, moreover, lies nearer to the mainlands on the west. For both these reasons it may be expected that the flora and fauna will be found to be the richest when it has been more thoroughly studied. Samoa (ix, 1–10) contains volcanic rocks and volcanoes of different ages and supports a large and endemic flora and fauna. In Tonga some of the islands are volcanic and probably not dissimilar to those in Samoa, though the insects remain almost unknown. But some of the islands, for instance, Tongatabu, consist of elevated coral, on which it may be supposed that the number of plants and animals will not be very great.

Relations with Indo-Malaya.

Examples.—One might say with truth that every writer who studied the insects of Samoa before the publication of the present work recognized that they were related to forms living in Melanesia and Malaya (see, for instance, Rebel, 1910), and this is consistent with what is known of the other animals and the plants (ix, 19 and 26). Those who have contributed to the present work are of the same opinion, or passively accept the view that the Samoan insects are Indo-Malayan in origin. Meyrick, for instance (iii, 67), expresses the view that the Microlepidoptera of Samoa are Indo-Malayan, and that they reached the central Pacific by way of Melanesia ; indeed, he goes farther than that and specifically says that there is no element derived from Australia and New Zealand or from America. Meyrick's views command particular respect because of his wide knowledge of the Microlepidoptera of Australasia and Oceania. The same view is expressed in the pages of this work by Prout, Beeson, Edwards, Berland and several other authorities. Moreover, all those contributors who have made a table * of the distribution of Samoan insects have shown clearly their origin from the west.

In the simplest case one finds that as a group of insects extends itself from west to east in the Pacific, some species or larger unit ceases to appear as each sea gap is passed. In studying the groups of insects which are absent from Samoa

* The following tables showing the distribution of insects in Samoa and other archipelagos have been published in this work :—Fulgoroidea, ii, 2 (Muir) ; most families of Heteroptera, ii, 83 (China) ; Miridae and Anthocoridae, ii, 194 (Knight) ; Rhopalocera, Samoa and Tonga only, iii, 6 (Hopkins) ; Heterocera (most families), iii, 173 and 176 (Tams) ; Heteromera, Bostrychoidea, Malacodermata, Buprestidae, iv, 68 (Blair) ; Cerambycidae, iv, 135 (Aurivillius) ; Curculionidae, iv, 249 (Marshall) ; Nematocera, vi, 24 (Edwards). There is also a table of distribution of Araneida, viii, 35 (Berland).

(p. 81) a number of examples were quoted ; but the insects which have reached Samoa show the same phenomenon, for instance, the genus *Papilio* extends eastwards through Melanesia and Fiji to Samoa where a single species (*P. godeffroyi*) is found : east of this the genus is unrepresented. There are other representatives among the moths : *Mnesiloba*, which is a subgenus of *Eupithecia* (Geometridae) is found from the Nilgiris and Ceylon eastwards to Samoa and Tonga. The genera *Scopula* and *Sterrha* (Geometridae) are very widely distributed, though absent from the south of South America, New Zealand and Hawaiia ; in Malaya and Melanesia there are several species, and in Samoa one only. Among other orders of insects many examples could be quoted, but two from the Diptera may suffice (Tabanidae and Culicidae). In the Tabanidae there are a number of genera and species in the Malay Islands and several species of *Tabanus* are known from Melanesia and Fiji ; in Samoa there is a single endemic species (*T. samoensis*), but no representative of the genus is known from Tonga, eastern Polynesia or Hawaiia (Ferguson, 1927).

The mosquitoes (Culicidae) exhibit the same type of distribution. These insects provide admirable material for the study of zoogeography, for they were never collected until 30 to 40 years ago, so that there are few erroneous records, and since that date they have become well known and been studied more thoroughly than any other group of insects in the Pacific. The geographical distribution of some of the species within Oceania was fully discussed a few years ago (Buxton and Hopkins, 1927) ; since then much new work has been published, which has been summarized by Edwards (1932a) and Taylor (1934)* : it is therefore unnecessary to give detailed references. In Table 4 I have set out the geographical distribution of all those sub-genera of Culicinae which are recorded from any islands east of New Guinea. The subgenera are those accepted by Edwards (1932a). The islands are arranged from west to east ; the subgenera have been arranged to show their extension eastwards, those with the most

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* Taylor's list is so useful that I must be pardoned for calling attention to one or two omissions and statements which appear to be erroneous. *Mansonioides uniformis* is recorded from Solomon Islands (Edwards, 1926c), and there are female specimens in the London School of Hygiene and Tropical Medicine, from Rabaul, New Guinea (Backhouse). *Aëdes* (*F.*) *kochi*, type form, record from Tonga quoted by Taylor refers to var. *samoana :* type form occurs in Fiji (Edwards 1926c). *Aëdimorphus vexans* is known from New Hebrides, Tonga, Ellice Islands (and Cook Islands doubtfully), see Buxton and Hopkins (1927). The record of *Anopheles* (*Myzomyia*) *punctulatus* from New Caledonia is an error, and rather an important one ; it seems to have originated in Edwards (1932a) and been copied by Taylor.

TABLE 4.

Giving the distribution of all subgenera of mosquitoes (Culicinae) known to occur east of New Guinea.

SUBGENUS.	BISMARCKS.	SOLOMONS.	NEW HEBRIDES.	NEW CALEDONIA.	FIJI.	SAMOA.	TONGA.	ELLICE.	SOCIETY IS.	COOK IS.	MARQUESAS.
Stegomyia	+	+	+		+	+	+	+	+	+	+
Culex	+	+	+		+	+	+	+	+		
Aëdimorphus	+		+	+	+	+	+	+		(?)	
Finlaya	+	+		+	+	+	+				
Tripteroides	+	+			+						
Mimetomyia		+	+	+	+						
Uranotaenia	+	+			+						
Coquillettidia				+	+						
Aëdes	+	+	+								
Ochlerotatus				+							
Mucidus		+		+							
Myzomyia	+	+	+								
Lophoceratomyia	+	+	+								
Armigeres, Lutzia, Rachisoura, Geoskusea, Mansonioides, Culiciomyia, Mochthogenes	+	+									
Megarhinus *	+										
Hodgesia	+										

extended distribution in Oceania heading the list. I have omitted the distribution of *Culex fatigans* and *Aëdes aegypti* (*argenteus*), for we know that these are species of recent artificial introduction. It will be seen that mosquitoes are an excellent illustration of the general rule that the fauna of the Pacific spreads out from the west towards the east. The farther one goes towards the east, the thinner is the fauna, and there is no evidence of the development of important endemic faunas in the eastern Pacific: moreover, there are very few instances in which a subgenus is found in the eastern Pacific, but is absent from islands more to the west. It must, however, be admitted that much fine detail

* The record of *Megarhinus inornata* from Funafuti, Ellice Islands (Rainbow, 1897), need not be seriously considered.

is lost by tabulation under subgenera. The table, for instance, fails to show that in Samoa and in Tahiti, endemic species of *Culex* (*C. samoaënsis* and *atriceps* respectively) have developed : we do not know from what member of the genus *Culex* these endemic species have originated. There are one or two gaps in the table (e.g. in *Mucidus*, *Ochlerotatus*) which may be due to the imperfection of our present knowledge ; some of them, for instance, the absence of *Finlaya* from the New Hebrides, are probably genuine, for I failed to find Aëdes (*F.*) *kochi* during several months spent in that archipelago. The irregularities in the distribution of the subgenera of *Mansonia* are probably also genuine and not due to present ignorance, for the distribution of these mosquitoes may be assumed to depend on some aquatic plant.

As the fauna has spread in this simple manner from west to east, there is much similarity between the insects of Samoa and those of Fiji and Tonga : for instance, Tams names 5 Samoan moths which are represented by subspecies in Fiji and 2 which are represented by subspecies in Tonga : he adds a list of other Samoan moths which have very close relations in Fiji or Tonga. Prout mentions a number of Geometridae which appear to be common to these three archipelagos, and not found outside them ; other examples could be discovered in other orders of insects. It would not be difficult to extend the circle of study, and name insects found in these three archipelagos, and also in Tahiti, or New Caledonia or the New Hebrides.

A " Central Polynesian " distribution has been observed in the Arachnida : among 81 species known from Samoa, no less than 25 show relationship with Fiji, Tonga and other island groups in Polynesia. This resemblance is what one would expect from the proximity of these archipelagos to one another and appears to be easily explained by the existing geography. Berland (viii, 41), however, has expressed the view that we have here an indication of an ancient land mass of which Samoa, Fiji and Tonga are the remains. More recently (Berland, 1934b) he has examined collections from several other parts of Polynesia, which have led him to the conclusion that the fauna of the whole of Polynesia, including the Hawaiian Islands, is so uniform as to suggest that these islands are but the fragments of a single mass of land. Berland's view, derived from a study of spiders, is similar to Pilsbry's, founded on Mollusca (ix, 23). But I feel that perhaps Berland has hardly considered the difficulties which are revealed by a general study of the distribution of plants and animals, of the ocean depths, and of the geology.

ANOMALIES.—We find then that the majority of Samoan insects have reached their present home from the west, and that their resemblance to the insects of Fiji and Tonga is accounted for by their geographical proximity to one another. But there are certain exceptions and anomalies: a number of insects occur in Samoa though they appear to be absent from Fiji and the islands to the west: there are also insects which are not known to occur in Samoa, but which are found in islands to the east, particularly in the Marquesas.

There are certain butterflies absent in Fiji and the islands to the west, but present in Samoa: at least three species are so distributed. Two of them, *Hypolimnas errabunda* and *Atella exulans*, are hill species in Samoa, with closest relatives in New Guinea (similar *Hypolimnas* being known also from the Solomons). It is possible that collecting in the mountains of Fiji or the New Hebrides might show their existence in these intervening areas. But the third butterfly, *Euploea schmeltzi*, occurs in the lowlands and is absent from the area between Western Samoa and the Loyalty Islands. Moreover, within the Samoan archipelago it occurs commonly in Upolu and Savaii but not in Tutuila or the Manua Group, where its place is taken by another member of the genus not found in Upolu and Savaii. The distribution of *E. schmeltzi* is extremely difficult to understand, for it has actually been observed flying out to sea to the small island of Nuutele, which lies about a mile from the coast of Upolu, though it has never been discovered on Tutuila, which is only 45 miles away. There are similar anomalies of distribution among those butterflies which have developed endemic races (Table 2, p. 72); here again a sharp distinction between Western Samoa and Tutuila is evident in three different species. The view has been put forward (Hopkins, iii, 5) that the form found in Tutuila has been derived from Tonga and Fiji, but that the form in Western Samoa shows some relationship with islands as far away as New Guinea.

Certain insects which appear to be absent from Samoa but which are known to occur in eastern Polynesia, particularly in the Marquesas, are of great interest because their distribution raises difficult questions of zoogeography. Of those which occur in the Marquesas the small Simuliid midges are the most remarkable. It appears (Edwards, 1932b, 1933a and b) that there is a single species of *Simulium* which is widely distributed in the New Hebrides and Fiji: no representative of the genus is known from Samoa, Tonga (or the Hawaiian Islands). In Tahiti there are three endemic species, and in the Marquesas there are three different

endemic species. These six species form a compact group within the widely distributed subgenus *Eusimulium*, and it is definitely Edwards' opinion that they are derived from the west and that they have not affinities with Simuliidae in America. It seems then that these midges have spread eastwards across the Pacific but have in some way failed to colonize Samoa. An alternative is possible. It may be that members of the genus still remain undiscovered in the Samoan Islands in some of the hundreds of gullies in the forests, many of which have never been entered by a European. In Savaii, particularly, the forest is almost unknown except round the coast. But against this view that there may be Samoan species of very limited distribution is the fact that those species which occur elsewhere in the Pacific are not extremely localized, as can be seen from the large number of localities from which they have been collected. While I admit the possibility that *Simulium* may occur in Samoa and remain to be detected later, I incline to the view that it is really absent.

One may also call attention to the absence of the butterfly *Libythea* from Samoa. I understand that a single species (*L. geoffroyi*) is widely distributed from the Malay Peninsula to the Solomon Islands and the Loyalty Islands (Riley, letter). But eastward of that, in Fiji and Polynesia, there is no record of any species, though the butterflies of several archipelagos appear to be well known, except *L. collenettei*, which occurs only on Nuka Hiva in the Marquesas (Poulton and Riley, 1929). *L. collenettei* appears to be related, but not closely, to *geoffroyi*, but to present a number of unusual and perhaps archaic features.

Reference has been made elsewhere (p. 79) to the curious distribution of the Pyralid genus *Scoparia*. These moths appear to be absent from the whole of Melanesia, Fiji and Samoa ; it may certainly be claimed that the small moths of Samoa have been carefully collected and studied. A few endemic species are known to occur in the Marquesas, Tahiti, Rapa, and in the Hawaiian Islands there are many endemic species. The similar anomalous distribution of an ant-lion, *Eidoleon bistrigatus*, has been mentioned (p. 81) ; the insect has a very wide distribution which embraces Tahiti, Raiatea, the Tuamotus, the Hawaiian Islands, Fiji and Australia, but it appears to be absent from Samoa. The distribution of *Rhyncogonus*, a genus of weevils, is rather similar. There are 33 species in the Hawaiian Islands, some of them having been found even on the outlying islands (Laysan, Wake, etc.) : in the Marquesas there are 6, in Rapa 1, and the Kermadecs 1 (Van Dyke, 1932). These weevils are not

known from Fiji, Samoa, etc., in spite of the considerable collection made in Samoa.

These curious geographical facts are capable of several interpretations, but we cannot discuss them without considering what relations there may be between the insects of Samoa and Hawaiia, for it is now apparent that the Hawaiian and Marquesan faunas have notable points of resemblance.

Relations with Hawaiia and the Marquesas.

Hawaiia.—The remarkable and highly endemic fauna of the Hawaiian Islands was the subject of the classical "Fauna Hawaiiensis," published in the early years of this century and summarized by Perkins in 1913. Since those days, investigations in other parts of the Pacific have tended in the main to confirm the conclusion that the fauna of Hawaiia stands quite by itself in the world. But it is now known that one or two groups of insects, formerly believed to be endemic to the Hawaiian Islands, have a wider distribution. A considerable number of them are found also in the Marquesas (Mumford and Adamson, 1934). So far as Samoa is concerned, the most interesting among these insects is *Proterhinus*, a genus of minute beetles distantly related to the weevils. It was at one time supposed that the members of this genus were confined to the Hawaiian archipelago, where more than 100 species are known to exist; but within recent years 1 species from Samoa, 1 from Enderbury Island (Phoenix Group) and 2 from the Marquesas have been described. Moreover, the view is now held that *Proterhinus* is not so peculiar as to justify the maintenance of the family Proterhinidae, and it has recently been sunk in the Aglycyderidae, the other members of which inhabit New Zealand and the Canary Islands (Perkins, 1932): *Proterhinus* is one more example of the category of minute beetles widely distributed in some tropical islands, and in this particular case greatly developed in Hawaiia. Elsewhere in this work I have called attention to other examples of this type of distribution, which is perhaps due to the effect of wind (p. 43). In this connection I observe that Arrow has recorded from Samoa 5 minute beetles belonging to the families Corylophidae, Cucujidae, Mycetophagidae and Dermestidae, previously thought to be peculiar to Hawaiia.

A few other examples of groups of insects now known to occur in Samoa though previously regarded as endemic to the Hawaiian Islands have been found.

Perhaps the most interesting is the genus *Austrochrysa* (Chrysopidae), with one endemic Samoan species, and a Hawaiian species which is perhaps referable to this genus. Mention may also be made of *Libnotes perkinsi*, a Tipulid originally described from Hawaiia and since discovered in Tahiti, Fiji and Samoa. In view of its distribution it is not impossible that the early stages of this insect have been carried about the Pacific by Polynesians among the roots of growing plants. The distribution of the woodlouse, *Ligia perkinsi*, should also be mentioned: in the Hawaiian Islands it occurs high in the mountains, where it was supposed to be endemic until we discovered it on rocks on the shore of the islet of Namua, off the coast of Upolu. But such an anomalous distribution as this must surely be due to our present ignorance.

We have mentioned a few points of resemblance between the Samoan and the Hawaiian Islands, but the points of difference are almost innumerable: indeed, one may say that with the exception of *Proterhinus*, none of the genera which have developed great numbers of endemic species in the Hawaiian Islands are represented in Samoa. One may take a single example. Tams has observed that of the 52 moths which have been recorded in the Hawaiian Islands but are not endemic there, 6 only are known from Samoa: all of them are either cosmopolites or pests of agricultural crops. There are also very great differences among the families and higher groups. From a consideration of all the facts, I think we may conclude that the points of positive resemblance between the Hawaiian Islands and Samoa are very few. There are points of negative resemblance, such as the absence of certain orders (p. 76) from both, but these are explained by saying that both archipelagos have a typical oceanic fauna. Almost the same degree of negative resemblance might be found between the fauna of Samoa and that of the Seychelles, between which no zoogeographical connection can be supposed to exist.

Marquesas and "Palaeonesia."—We can now consider the relation of the Samoan fauna to that of the Marquesas, which in turn has certain points of resemblance to the fauna of the Hawaiian Islands. As we have seen, it is almost certain that a number of insects—*Simulium*, *Scoparia*, *Libythea* and others—are really absent from Samoa though they occur farther east in the Marquesas; and yet competent authorities tell us that the forms found in the Marquesas have certainly been derived from the west and not from the American shores of the Pacific. It will be observed that none of these genera is endemic in Polynesia and that in none of them, except perhaps the *Libythea*, are the

Marquesan species very peculiar or primitive. It should also be remembered that certain of these insects, for instance *Scoparia*, extend their range to the Hawaiian Islands. But there is little relation between Hawaiia and Samoa, though the genus *Proterhinus*, formerly thought to be endemic in Hawaiia, has now been found in several other archipelagos, including Samoa.

It would not be fitting to give much space to the zoogeographical problems of eastern Polynesia, which are not strictly relevant here: but it is necessary to make reference to the theory of Palaeonesia. Meyrick (1926) investigated a collection of small moths from Rapa, an island so small and remote that he could not believe that the moths had reached it by air. He therefore suggested that there must have been a much larger land mass during the Eocene, and he postulated an elevation of 12,000 feet of the floor of the Pacific which would give an island 400 miles long. Such an island might help to account for the presence in Rapa of insects showing affinities with Fiji and eastern Australia. At a later date the same author (Meyrick, 1928) examined a collection of Microlepidoptera from the Marquesas, Society Islands, Tuamotus and Austral Islands. This led to some modification and extension of his view, for he found that he required a much larger land mass, to which he then gave the name Palaeonesia. He also supposed that a different elevation of the floor of the Pacific had occurred farther west, which greatly increased the area of land in that region. But in spite of this, the Palaeonesian genera are thought to have reached their present home by some route which avoided those large islands, the hypothetical position of which seems to be directly in their hypothetical path. Indeed, it seems to be an essential part of Meyrick's view that there is a fundamental dissimilarity between the faunas of western and eastern Polynesia, so that in this second paper the connection with Fiji is no longer sought for. Subsequently, Meyrick (1929) examined a collection of Pyrales from the same area in eastern Polynesia. In their distribution he found confirmation of the previous existence of Palaeonesia, and in particular he referred *Scoparia* to the "Palaeonesian period," not yet defined.

The present writer can claim no knowledge of the Microlepidoptera, but he has examined the evidence put forward by Mr. Meyrick and endeavoured to relate it to our general knowledge of Oceania. He is led to a less elaborate hypothesis by the following considerations:

(1) In his first paper (1926), Mr. Meyrick stated that "a rise of 12,000 feet in the bottom of the South Pacific is required." In the second (1928) he defined Palaeonesia as a "land area to include the whole of this region of the Pacific

from Rapa to the Marquesas, and from Pitcairn Island to the Society and Cook Groups." The student of maps will discover that this handsome piece of territory extends about 20° by 30°, say 1,200 by 1,800 miles. No consideration seems to have been given to the geophysical problems involved in raising this area 12,000 feet.

(2) Mr. Meyrick cannot believe that so remote and minute an island as Rapa could have been colonized from the air, even over vast periods. This is not a matter on which it is possible to dogmatize, but there is positive evidence of the wind carriage of minute insects (p. 43), and there are a number of small beetles and other insects which appear to be very widely distributed in the tropics by some natural agency (p. 44). It is possible that the smallness and fragility of the microlepidoptera might aid their dispersal.

(3) It is certainly true that the distribution of some of the Microlepidoptera is difficult to explain in relation to existing geography ; *Scoparia* is an example (p. 79). Another distributional anomaly is found in the Pyralid genus *Aspithra,* of which 1 species is found in Ceylon and the other 4 in the Marquesas. Another quite different problem is afforded by the Tortricid *Dichelopa*, with 14 endemic species in eastern Polynesia, 6 in eastern Australia and none elsewhere. The Tineid *Gracillaria* presents a difficulty of another type : its distribution is nearly universal, species occurring in New Zealand, Rapa and Hawaiia, but it appears to be absent from Fiji and Samoa. The reader will observe that Palaeonesia would help to explain the distribution of *Scoparia*, but it does not appear to reduce these other anomalies.

(4) But though these difficulties occur, many of the Microlepidoptera conform to the general rule that the fauna of Oceania has spread out from the Asiatic side, becoming thinner and thinner as each sea gap is crossed. For instance, the Tineid genus *Labdia* is abundant in the Indo-Australian region and species, most of them endemic, have been collected in the New Hebrides, Fiji, Samoa, Tonga and the Ellice Islands. That represents approximately the eastern limit of *Labdia* (cf. the distribution of *Papilio* and other insects, p. 84). On the other hand, *Imma* and *Decadarchis* (Tineina) and *Bradina* and *Margaronia* (Pyrales) show affinities with Indo-Malaya, but they have developed endemic species not only in the west of the Pacific, but also in eastern Polynesia. In the distribution of such genera one sees an essential similarity between the fauna of those groups which Mr. Meyrick would include in Palaeonesia and that of Samoa, Fiji and the islands to the west.

(5) To sum up, the Marquesan insects are undoubtedly peculiar and highly endemic, as are those of Hawaiia, but there is evidence among the Microlepidoptera and elsewhere indicating that the fauna came from the west and that it is essentially like that of Fiji, Samoa, etc. I believe that the zoogeography of Oceania, including eastern Polynesia, can be explained by reference to the map as it is to-day. Certain anomalies undoubtedly exist and will perhaps continue to trouble us, even when our knowledge of these faunas is much more complete than it is at present. Some of these may be explained if we consider the possibility that the insects of the Polynesian archipelagos arrived by different routes. One must remember that in this part of the world the anti-trade wind blows steadily from the west at a height of a few miles, while the trade winds, which are doubtless more important because they are at ground level, blow from the east or south-east for most of the year (ix, 18). Here then we have two natural machines of great power and regularity tending to move animals and plants in opposite directions. It is a matter of fact that most of the fauna has come from the west, but it may be supposed that some of it has been carried back again towards the west, perhaps over a different route.

Relations with Australia and America.

Australia.—We have made it clear that the insects of Samoa have come from the west and that the fauna of Melanesia and at least the greater part of Polynesia is derived from Asia. It is perhaps best to describe this fauna as "Indo-Malayan." The word "Indo-Australian" is sometimes used but is misleading because it tends to suggest a resemblance to the fauna of the Australian continent.

But though the relation between the animals of Oceania and continental Australia is slight, one or two definite points of resemblance exist. We have referred elsewhere (ix, 22) to the honeysuckers (Meliphagidae), a family of birds which spreads outwards from Australia and Papua through Melanesia and much of Polynesia. One or two examples of similar distribution among the insects are known. They are important and interesting by reason of their rarity. The most remarkable of these are the Tachinidae of the genera *Rutilia* and *Rhinomyiobia*. In Samoa there are two endemic species of *Rutilia* and there is one in Fiji. The members of the tribe Rutiliini are almost exclusively Australian, though one is recorded from China and one or two from the Malayan area: there are none in New Zealand. Apart from the fact that the Samoan and Fijian

species are endemic, so far as we know at present, it would be difficult to suppose that they had been introduced by man, for their early stages are probably parasitic on larvae of Coleoptera. On every ground, therefore, we conclude that they are native. The other Tachinid, *Rhinomyiobia plumifera*, is rather similar in distribution. The species is peculiar to Samoa and Fiji, and the other members of the genus are mainly Australian. Several other Samoan insects of different orders show a similar relation to the Australian continent. The genus *Phycomorpha* (Copromorphidae, Tineina) contains at present two species, one from Sydney, New South Wales, and the other from the hills of Upolu, Samoa. The only Samoan *Crambus* (Crambidae, Pyrales) is a species known to occur in Fiji and Australia. Tams has called attention to five species of moths which are known only from Samoa and Australia, but he states that the material is insufficient and that more careful and critical work is necessary before we can be certain in four of these cases. The remaining moth is *Phlegetonia fasciatrix*. There are also points of resemblance between the Samoan Carabidae and those of Australia : four of the fifteen Samoan species are known to occur in Australia, but it should be remarked that little is known of the Carabidae of neighbouring archipelagos, for instance, Fiji and Melanesia : for the same reason we must be cautious in attaching importance to the distribution of *Crambus* and *Phycomorpha*. The distribution of *Chrysopa* appears to stand rather by itself. It seems that certain members of this genus have a very wide range, and *Chrysopa* itself is nearly world-wide. Why this should be so is not known, and perhaps the facts have not yet been sufficiently studied, but we observe that four out of the nine species of *Chrysopa* which occur in Samoa are also recorded from Australia.

America : Wegener's Hypothesis.—It is already clearly shown that the insects of Samoa are derived in great part from the west ; to myself it seems clear that the boundary of this Indo-Malayan element lies far to the east of Samoa, and that the region embraces all Polynesia including the Marquesas. But it might be asked whether there is no American, or eastern, element among the native Samoan insects ? From a consideration of the articles which specialists contributed to this work, it seems that very few insects of American origin could be quoted and that for the most of them the evidence is of doubtful value. Arrow (iv, 36), for instance, recognizes an American element in the fauna, but perhaps some of his examples are insects of very wide distribution at present not sufficiently collected : one has probably been introduced into Samoa, and one at least is very minute so that it may fall into the wind-carried group. Beeson

(iv, 245) shows that among the 34 Scolytidae, only one species, *Xyleborus confusus*, is probably derived from America: but the evidence is of indefinite value, for the insect, which has a very wide distribution in the tropics but is apparently absent from the Indo-Malayan region, is known to feed on a number of plants of economic importance (*Cocos*, *Manihot*, *Hevea*). Among the Diptera a remarkable insect is *Zygothrica samoaënsis* (Drosophilidae). This insect, endemic to Samoa, exhibits the sharply defined peculiarities of its genus, all the other species of which are confined to South America. It is possible that the anomalous distribution of this minute fly may be due to wind currents. One or two other examples of insects apparently of American origin have received notice in the text, but they are not convincing. There is, for instance, an Asilid doubtfully referred to the Central American genus *Atonia*, but represented in the Samoan collections by a fragmentary specimen. One might also mention *Sarcophaga peltata*, but it may well have been recently introduced; moreover, its specific identification is not beyond dispute, and the view is expressed by Malloch (1932) that the American *S. peltata* Aldrich does not occur in the Marquesas and Tahiti (and by implication in Samoa), and that the Polynesian specimens are referable to *taitensis* Schiner, which is probably native to these archipelagos.

We conclude that very few Samoan insects show affinities with America. It is perhaps appropriate to consider the theory of continental displacement put forward by Wegener, but it is unnecessary to discuss it fully for its scope is mainly geographical or geophysical; its biological applications relate particularly to the fauna and flora of those continents which now lie round the Atlantic and Indian Oceans. But so far as the Pacific is concerned, we observe that Wegener upholds the view of the permanence of this ocean at least since the Upper Carboniferous Period. He believes that since that time the Pacific has been narrowed from two directions: Australia and New Guinea have broken away from the east extension of the Antarctic region and come to occupy their present position on the flank of Malaya and Melanesia (a movement with which we are not now concerned); during the same period the American continents have swung to the west from a fixed base in the Arctic regions so that at the Equator the American coast of the Pacific is some 30° (say 1,800 miles) west of the position which it occupied in the Upper Carboniferous Period. Nothing that could be discovered in the fauna of Oceania is likely to prove or disprove this theory, but we may say that what is known of the distribution of animals in

the Pacific is consistent with the view that that ocean is permanent. Moreoever, if America once lay farther to the east than it does at present, that helps to explain the absence of American plants and animals from Hawaiia (Wegener, 1924, p. 84) and from Polynesia in general.

IV. SUMMARY OF CONCLUSIONS

The collection of insects from Samoa is far from complete and not equally representative of all orders (p. 37), but it is certainly a sufficient foundation for general conclusions. But it must be remembered that these can only be tentative, because so little is known of the fauna of other parts of the tropical Pacific. It is a matter of regret that geological evidence is, and must perhaps always be, almost negligible in Polynesia, so that we are compelled to rely to a great extent on faunistic material.

The study of a large collection of animals or plants from an archipelago may be expected to supply information on several points of interest. One should, for instance, be able to decide whether the islands are oceanic or continental, by which we mean whether they have always existed as small points of land in a great ocean of water or whether at one time they were part of a large mass of land, perhaps connected with existing continents. One should also be able to discover from what direction the fauna reached the islands and perhaps by what means or channel it came.

Oceanic or Continental ?—Evidence of possible connection with continental masses of land may be obtained by considering what groups of animals are absent as well as what are present. In the Samoan insect fauna a number of remarkable and doubtless significant absentees have been observed. Of the 23 recognized orders of insects, 5 have not been found in the archipelago. Of these, 2, the Protura and Strepsiptera, may perhaps be discovered when more skilled and specialized collecting is undertaken, but we may probably accept it that the other 3, the Plecoptera, Embioptera and Mecoptera, are absent. In addition to these 5, the Siphonaptera are only represented in Samoa by species which have apparently been introduced by human agency, and the Trichoptera and Plectoptera (Ephemeroptera) are each represented by a single endemic species. The very great bulk of the fauna is therefore made up of representatives of 15 of the orders. Study of those orders which are absent

reveals remarkable points of similarity to the faunas of the Hawaiian Islands and the Marquesas: the resemblance to the fauna of the Seychelles is just as striking and even more remarkable, for it cannot be due to any local cause (p. 76). The absentees among the families and lesser groups of insects have been discussed at some length. The facts lead to the general conclusion that the Samoan Islands are oceanic; since certain widely distributed families are absent from Samoa, other families are over represented in proportion to the whole fauna (p. 77).

Let us now make a study of the insects which are present, and particularly of the endemic species. 1,603 species are known to occur in Samoa, of which 49% appear to be endemic. The corresponding figures for the Hawaiian Islands are 4,620 species, 81% endemic, and for the Seychelles 2,090 species, 65% endemic (p. 66). It must be admitted that the percentage of endemic species in the Samoan fauna may be modified with an increase in knowledge, but it appears to be unlikely that it will be greatly raised. One characteristic of the fauna of such an archipelago as Hawaiia is the development of complex groups, many of them containing a very large number of closely related species. In this respect the Samoan fauna is poorer than that of the Hawaiian Islands and probably the Marquesas; in Samoa such groups are rather few, and not generally very complex, but the phenomenon does occur and instances are quoted among the Tineina, Tipulidae, Curculionidae, Zygoptera, etc. (p. 68). Where such endemic complexes occur, it is generally found that many of the species are found only on one island in the archipelago. But in this matter evidence must be full before it can be convincing. If an insect has been collected on only one island, we can only admit that it is absent from the others if it was obtained on many occasions or was so familiar that its local distribution was remarked by those working on the spot. Among the Samoan insects there are only a few examples which are undoubtedly confined to part of the archipelago. There are, for instance, three Rhopalocera which exhibit racial differences between the form found in Western Samoa (Savaii and Upolu) and that found in American Samoa (Tutuila and Manua). The familiar and conspicuous moths of the genera *Chrysaeglia* and *Deilemera* are also certainly confined to particular islands. It has been observed that nearly always, when island endemism exists, the line of division between species or races is that separating Western from American Samoa (p. 72). The endemic fauna of an oceanic island sometimes contains animals, the systematic position of which is anomalous, but among the Samoan

insects no examples could be quoted. It should also be noticed that the systematists who have dealt with the Samoan material have not found it necessary to erect any new tribe or subfamily.

The study of the insects, both of those which are absent and of those which are present, leads to the same conclusion, that the fauna of Samoa is oceanic. But it is not so peculiar (and therefore perhaps not so ancient) as that of the Hawaiian Islands, or probably of the Marquesas. But though I have no hesitation in stating that the fauna of Samoa is typically oceanic, I must admit that there are certain facts which are difficult to reconcile with this conclusion. For instance, it will be remembered that we collected a peculiar Locustid, *Rhaphidophora rechingeri*, in a cave in Upolu. The insect lived in total darkness upon heaps of bats' dung, and was clearly specialized for existence in a cave, lacking wings and eyes. Its affinities are with the west, and a number of other and equally specialized and peculiar members of the group have been found in Malaya, etc. It seems to be almost impossible to imagine how this insect, specialized for life in a cave, could have reached the Samoan Islands by any method of transport overseas. The same difficulty confronts us when we consider the distribution of many other insects, of which the habits or breeding places are narrowly specialized; for instance, the Anthomyid, *Limnophora immaculiventris* and the Gryllid, *Anaxipha hopkinsi*, found together skating over the surface of streams; parasitic insects, gall-makers, and all specialists fall in the same group; it is difficult to think how such insects or their ancestors could have been brought across the ocean, presumably from an equally specialized home in some archipelago to the west.

Origin.—It is clear, and generally admitted, that the fauna of Samoa is essentially Indo-Malayan, and that the fauna of Oceania, or at least the greater part of it, has spread out from the west, passing through Melanesia and Fiji into Polynesia, and becoming poorer with the passage of each area of sea. There is no one point at which the fauna becomes suddenly impoverished, and there is no faunistic evidence to demarcate the edge of an old continent at any particular point. It may be added that within the distribution of a genus or family, the general rule is that the number of species may be considerable towards the west, whereas only a few occur where the eastward limit is approached.

As would be expected, there are a number of points of similarity between the insects of Fiji, Samoa and Tonga, owing to their geographical proximity, and their nearly equal distance from the large Malay Islands; but there are also many

differences between them and it would not serve a useful purpose to delimit a subregion. I fail to find evidence supporting the view which has been enunciated that these three archipelagos are the remains of an old land mass (p. 86).

The general rule that the fauna spreads evenly from the west to the east is subject to certain exceptions. For instance, the butterfly, *Euploea schmeltzi*, has an anomalous distribution, for it occurs in the Loyalty Islands and Western Samoa but not in Fiji. Several insects are absent from Samoa (and not merely unobserved) though they occur in islands to the east. The butterfly genus *Libythea* extends from Malaya to Melanesia, including the Loyalty Islands, but it does not occur in Fiji or anywhere in Polynesia except that an endemic species exists on one island in the Marquesas. The distribution of the Pyralid genus *Scoparia* is perhaps even more remarkable, for it is absent from Melanesia, Fiji and Samoa, but present in eastern Polynesia including the Hawaiian Islands. Other examples have been quoted from among the Diptera and Coleoptera (p. 87).

The existence of these insects in the Marquesas and of some of them in Tahiti, Rapa, etc., and their absence from Samoa and generally from Fiji seemed to Meyrick to indicate a fundamental difference between the fauna of western Polynesia, which is Indo-Malayan, and that of eastern Polynesia. A consideration of the distribution of the Microlepidoptera led him to suppose that a large land area once existed in eastern Polynesia, to which he has given the name Palaeonesia (p. 91). His hypothesis certainly helps to explain the distribution of *Scoparia*, though it leaves a number of other riddles unsolved, and it seems that the very great geological difficulties have not been considered. To the present writer it appears that, though certain anomalies exist, the fauna of eastern Polynesia resembles that of western Polynesia in essentials, though certain groups are absent. It appears, also, that the insects may well have reached their present home at a time when land and water were distributed approximately as they now are (p. 93).

The recent increase in our knowledge of the insects of Samoa has shown that a few groups of insects occur in these islands which at one time were thought to be peculiar to Hawaiia, but in the main the fauna of the Hawaiian Islands stands by itself and shows little resemblance to that of the rest of Oceania, though there are certain notable points of resemblance to the fauna of the Marquesas (p. 89).

Though the Samoan fauna is clearly Indo-Malayan, one or two characteristic

Australian groups have reached Samoa, apparently by natural means. The best example is perhaps the Tachinid genus *Rutilia*, but there are one or two among the Lepidoptera. These insects with Australian affinities are very few compared with the rest of the fauna, but the relation to Australia is definite and extremely interesting (p. 93).

In the systematic Parts of this work, several insects of American affinities have been mentioned, but the importance of most of them is slight for their distribution may be due to commerce (p. 94). One of the most interesting examples is a Drosophilid (*Zygothrica*), but it is perhaps one of those small insects with a very wide tropical distribution which may be due to carriage in the upper air. It seems, therefore, that among the native Samoan insects the American element is very small or perhaps non-existent ; this is consistent with the views of Wegener, who believed that the Pacific has existed for very long geological periods, but that there has been a tendency for it to become narrower, so that at earlier epochs Samoa was even farther from America than it is now (p. 95).

Admitting that the insect fauna of Polynesia is oceanic and derived from Indo-Malaya through Melanesia, it is pertinent to inquire how the existing forms of life or their ancestors crossed the oceans and reached their present homes, so many of which are minute islands. These questions have puzzled zoogeographers since the days of Wallace, and we are not yet in a position to answer them, though knowledge is advancing in certain particulars. We now know that, though the surface currents and trade winds appear to hinder the spread of insects from the Asiatic side into the Pacific, there is a great stream of anti-trade wind at no great altitude. This blows and has blown all down the ages, and might well carry insects and other forms of life eastwards (p. 18). Recent work has shown that a considerable number of insects occur in the upper air (p. 43) and that there are species whose minute size has apparently assisted their carriage by wind so that they are distributed very widely in the tropics (p. 43). It seems, therefore, that we may suppose that wind, and particularly the currents of the upper air, are much more important agents in distributing small insects than we have realized. I venture also to suggest that the student of insect distribution has given insufficient attention to that interesting animal, Man. It is clear in Oceania that the wanderings of peoples before the coming of the European had a considerable effect on the distribution of plants and insects, and a knowledge of the life of the Polynesians, and particularly of their

crops and of the use which they made of vegetable products, assists one to distinguish organisms which may have been distributed by them.

But even if we have discovered something of the importance of the upper air and of human agency, it remains very difficult to understand how the insects of Polynesia reached their island homes ; it is impossible to assess the importance of the traditional floating log. But it appears that there are two ways in which the problem might be approached. The investigator of the future might try to discover whether the Samoan insects contain a particularly high proportion of forms breeding in unspecialized habitats, for instance, damp soil, dung and rotten wood, and whether those whose habits are specialized (insects inhabiting caves, associated with particular plants, parasitic on other insects, etc.) are few. An attempt should also be made to study the effect of sea water on all stages of the insects which have a wide distribution in tropical islands. Special attention should be given to those which are characteristic of the strand and which live in association with the strand plants whose seeds are known to survive long exposure to sea water.

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INSECTS OF SAMOA

AND OTHER SAMOAN TERRESTRIAL ARTHROPODA

LIST OF PARTS AND SYSTEM OF PUBLICATION:—

Part I. Orthoptera and Dermaptera. (Complete.)
„ II. Hemiptera. (Complete.)
„ III. Lepidoptera. (Complete.)
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„ VII. Other Orders of Insects. (Complete.)
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The work is published at intervals in the form of numbered fascicles. Although individual fascicles may contain contributions by more than one author, each fascicle is so arranged as to form an integral portion of one or other of the Parts specified above.

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